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The synecology of dense assemblages of the deposit-feeding Polychaete, Axiothella rubrocincta (Maldanidae)

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THE SYNECOLOGY OF DENSE ASSEMBLAGES OF THE DEPOSIT-FEEDING POLYCHAETE, *AXIOTHELLA RUBROCINCTA* (MALDANIDAE)

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TABLE OF CONTENTS

List of Tables

Table Page

Table Page

List of Figures

Figure Page

Figure Page

Introduction:

Interspecific interactions have been shown to play critical roles in determining the realized niches of species in marine rocky intertidal (i.e. Connell 1961, Paine 1966, Dayton 1971) and terrestrial (i.e. Harper 1969, Pianka 1973, Cody 1974) communities. In contrast, such interactions have not been clearly demonstrated as determinants of the distribution and abundance of marine intertidal soft-substrate organisms (however, see Levinton 1977). There are great physical differences between the rocky and mud-sandflat intertidal habitats. Some of these are wave exposure, sediment size (boulders to silts), penetrability and organic content of the substrate, frequency of log damage, and exposure to sunlight. Considering these physical differences and the fact that soft-substrate environments often support diverse communities, it is interesting to assess the role of biological interactions in structuring these intertidal communities. Previous work on this system primarily consists of descriptions of animal-sediment relationships and of food partitioning (i.e. Sanders et al. 1962, Mangum 1964, Reid and Reid 1968, Johnson 1971, Rhoads and Young 1971, Young and Rhoads 1971, Fenchel et al. 1975, Warren 1977). The role of interspecific interactions in establishing and maintaining infaunal distribution patterns on a sandflat in northern California

is reported here.

Axiothella rubrocincta Johnson (Maldanidae: Polychaeta) is a large (10 cm long) tubiculous deposit-feeder which forms persistent dense patches. Its feeding biology, population ecology(patch persistence, area, and density), and community ecology were studied from June 1975 to June 1977. Samples of the community were taken from within and on the outer edges of A. rubrocincta patches in order to determine whether certain species were more dense in either of these microhabitats. This determination was made for common surface feeders (polychaetes, crustaceans, bivalves) and burrowing deposit-feeders (polychaetes). Spionid polychaetes are common macrofaunal marine invertebrates living in soft-substrates, often in physical association with muddy sediments (Dorsett 1961, McIntyre 1961, Galtsoff 1964, Blake 1969, 1971, 1975, Whitlatch 1977). A 1 yr benthic sampling program revealed an increase in abundance of eight species of spionids on the outer edges compared with samples of equivalent tidal heights from within patches. A specific purpose of the study was to investigate the structuring mechanisms that produce and maintain the observed spionid distribution pattern. The mechanisms investigated included interspecific competition for limited resources (Cody 1974, Schoener 1974a), differential predation (Paine 1966) on spionids within A. rubrocincta patches, and physical unsuitability of

A. rubrocincta patches for spionids. These mechanisms are not considered to be mutually exclusive. The role of interactions between adult organisms and settling larvae has recently been emphasized by Woodin (1976) as the most important factor affecting the maintenance of discrete dense assemblages of infaunal organisms in soft-substrate communities. Woodin hypothesized that established adult infauna inhibit recruitment by larvae of their own and other species by preventing access to the substrate. The generality of this approach, which stresses interactions between age classes, was tested experimentally. Data were obtained on: 1)A. rubrocincta patch characteristics and individual feeding rates, 2)the A. rubrocincta community, 3)A. rubrocincta resource utilization and substrate modification, 4)spionid resource utilization and interactions with A. rubrocincta, and 5)spionid predator escape responses.

Study Area Characteristics:

The study was conducted on a south-facing sandflat, known locally as Lawson's Flat, in Tomales Bay, California (38°13'N and 122°58'W, Fig. 1). Tides are mixed semidiurnal and the salinity varies from 30-35‰ throughout most of the year (Johnson 1971). The flat, 1.6 km south of the bay mouth, has well sorted sands and an average slope of 1° (Johnson 1967). The original source of sand is from the dunes to the west. More complete descriptions of the area are given in Johnson (1965, 1967a, 1967b, 1970) and Daetwyler (1966).

The physical particulate properties of the Lawson's Flat substrate and its contained organic resources are related. An organic-mineral aggregate (OMA) consists of an organic matrix which varies in degree of compactness, and which has clay and silt sized mineral particles ($< 88\mu m$) embedded within it. The aggregates behave as particles when suspended in water. They are considered as a food source to deposit feeders because of their high organic content (Johnson 1974) and their meiofaunal and floral associates. OMA have been commonly found in this study and on both the Atlantic and Pacific American coasts from the intertidal zone to depths of 5000 m (Johnson 1977).

Adult Axiothella rubrocincta inhabit and primarily confine their activities within U-shaped sandy tubes.

The two tube openings function separately for sediment ingestion and defecation, creating a characteristic funnel and volcano-like reworked surface. Individuals of this species form dense patches. Three patches were chosen as study sites in June, 1975. Patch #2 was approximately 500 m northeast of the other patches and at an intermediate tidal height (Fig. 1). Patches #1 and #3 were 10 m apart at their closest points, but had almost no overlap with respect to tidal height. The range of exposure times varied from approximately 20% per week in the lower part of Patch #1 to as much as 65% per week in the upper part of Patch #3 (see Sediment Reworking Rates Section).

Methods:

I. *Axiothella rubrocincta* Patch Characteristics and Individual Feeding Rates

Sampling was conducted on the exposed sandflat at low tide. Four permanent stakes were placed in a rectangle around the outside of each *A. rubrocincta* patch. Patch tidal heights were determined by comparing high and low marks on the sandflat with tide table predictions. Two, 150 g sediment samples were taken from the top 3 cm of each patch in June, 1976 and were dry sieved through a Tyler screen series in 0.5 ϕ (phi) increments.

A surface defecation mound count for estimating density and patch area was adopted because collection of adult *A. rubrocincta* proved difficult. To test whether natural sand deposition could significantly alter the number of mounds visible from the surface, *A. rubrocincta* which were actively reworking sediment in laboratory sea water tables were covered with 5 cm of wet sand on three consecutive occasions and the time for mounds to reappear on the surface was measured.

A. rubrocincta patch area and within patch density were estimated monthly for 13 months. These measurements were not taken in Patch #1 in September, 1975, because algae covered the lower 2/3 of the patch. The left and right edges

of each patch were mapped at 6 m intervals for their entire lengths by laying a movable transect line across the patch. Surface counts of A. rubrocincta mounds were made within patches using a 0.25 m^2 quadrat. Between June, 1975 and February, 1976, quadrat samples were taken on a grid. Subsequently, quadrats were located using a table of random numbers. When patches expanded beyond the edges of the original quadrats (indicated on maps as nonenclosed areas) "outer" areas were not considered in the density-area estimate. The Wilcoxon two-sample test (Sokal and Rohlf 1969) was used to compare A. rubrocincta densities through time and space.

Sediment reworking rates of individual A. rubrocincta were studied during September 1975 using a modified technique described by Kudenov (1971, pp. 18-19). A small (1 cm diameter) hole was drilled in the side of each PVC cylinder to allow gradual filling and emptying with tidal changes. The PVC cylinders were placed to a depth of 6 cm over A. rubrocincta mounds. This depth was sufficient to fasten the cylinder while decreasing the probability of damaging the worm's tube. Grams of sediment reworked by each of five worms at four tidal heights was monitored for 7 consecutive days. Individual reworking rates (grams reworked per day/ % of the day submerged) were estimated for cross-intertidal comparisons. The % submergence/day was estimated from 12 direct observations of water position at fixed stations.

II. The *Axiothella rubrocincta* Community

The macrofauna inside and around the *A. rubrocincta* patches was sampled for a 1 yr period using a hand operated PVC suction core, 10 cm in diameter and 20 cm deep. The samples were sieved through a 0.5 mm screen and preserved in 7% formalin. The macrofauna was identified to species and preserved in 70% alcohol. The sampling dates were June, September, December 1975, and March and June, 1976. Each Study Site consisted of one *A. rubrocincta* patch and its outer surrounding edge. The sampling design was a three-way ANOVA with nesting and replication. The ANOVA treatments were Study Sites (3), Sampling Times (5), and Sample Location Within or Outside of an *A. rubrocincta* Patch (2). Stratified random sampling was performed by dividing each patch into an upper and lower half and taking three replicates in each half. For each of the "within patch" samples an outer sample, taken 1-2 m beyond the edge of the patch from the left and right sides at the same tidal height, was collected. Three-way ANOVAs were performed on the estimates of individual species and species group densities. One ANOVA involved data of the outside (left) and inside of the *A. rubrocincta* patches, while the other involved data from the outside (right) and inside. Two ANOVA comparisons were advantageous because species densities within the *A. rubrocincta* patches could be compared with two distinct

"outside of patch" habitats. In addition, two a priori comparisons (Sokal and Rohlf 1969) were planned for each ANOVA in order to test the effect of tidal height differences (Study Site #1 vs. #2 and #3) and the broad separation (Study Site #2 vs. #1 and #3) between Study Sites. A Student-Newman-Keuls test (Sokal and Rohlf 1969) was used to decompose significant "between Sampling Times" (Main Effect B) effects for densities of each species or species group.

III. *Axiothella rubrocincta* Resource Utilization and Substrate Modification

The response of four *A. rubrocincta* living in a simulated sandflat (26 cm wide and 31 cm long) to changes in surface OMA abundance was observed from March 11 to May 24, 1977. The reddish-brown flocculent aggregates (OMA) collect on stable sediment surfaces and particularly in depressions such as *A. rubrocincta* funnels (Kudenov 1971). Ten minute observations were made three times per week on worm feeding behavior. Tube position was noted during each observation. All visible OMA were pipetted from the worm feeding funnels on May 10 to determine the effect of its absence on worm feeding behavior.

Surface OMA abundance was measured from cultures containing *A. rubrocincta* for a 10 week period (May-July, 1976) in densities commonly occurring in the study area. Sediment used in the experiment was taken from an *A. rubrocincta* patch with a density of approximately 48 individuals/m^2. The sediment, taken from the upper 5 cm and containing the natural fauna, was placed in 25 cm deep containers and transported to the laboratory. Randomly chosen adult *A. rubrocincta* were placed in the containers in experimental densities. A field control was taken when the experiment began. There were four replicates per treatment. At the end of 10 wk, one 3 g sediment sample was randomly collected

from the top 1 cm of each treatment container and was treated with aPeriodic Acid Schiff stain (Whitlatch and Johnson 1974). This preparation stains most protein-carbohydrate, glycogen, and starch complexes red (Humason 1967), facilitating subsequent compositional descriptions of individual, randomly chosen particles. Four replicates were analyzed per treatment, with each replicate consisting of 50 particles. Comparisons using orthogonal polynomials (Keppel 1973) were made to detect linear and exponential changes in OMA abundance due to increased A. rubrocincta density.

IV. Spionid Resource Utilization and Interactions with A. rubrocincta

The gut contents of six Pseudopolydora paucibranchiata (Spionidae) were qualitatively analyzed for the presence of OMA. One hundred randomly chosen mineral particles were measured following treatment of the gut contents with warm H_2O_2 to destroy the organic material which aggregates the particles (Johnson 1974). OMA were collected at the same time from the substrate surface, using an eye dropper, for comparison with the gut contents. In the laboratory the intact OMA were also treated with H_2O_2, and 100 of the newly freed mineral particles which had been bound up within aggregates were measured.

The feeding behavior of tube-dwelling P. paucibranchiata was observed in dishes containing varied concentrations of OMA. The treatments ranged from total coverage of the surface by a thin OMA mat (0.5 mm) to one in which no OMA were detectable by eye.

The anterior ends of spionid tubes collected from muddy and sandy habitats were qualitatively analyzed for the presence of OMA. A quantitative PAS analysis, which describes individual OMA and mineral particles, was not possible because worms cement their tubes by a mucus secretion. Twenty five tubes involving six species of

spionids were investigated. One hundred randomly chosen mineral particles from two P. paucibranchiata tubes were measured following H_2O_2 treatment.

Spionid tude building behavior was studied in the laboratory by placing tubeless individuals of P. paucibranchiata on three treatment substrates (S). Each of the walled dishes (45 mm in diameter) contained a 5 mm deep substrate. Treatments S1 and S2 contained oven-dried sediment combined from the three A. rubrocincta patches and having the grain size distribution shown in Fig. 2. OMA was added to treatment S2 by suspending a large amount of OMA in sea water and pipetting up the mixture. After allowing the aggregates to settle in the verticle pipette for 1 minute, 3 ml were released into the S2 dish. S2 had visible clumps of OMA on the surface, but they were not abundant enough to form a continuous mat. Treatment S3 consisted of OMA but no additional A. rubrocincta patch sediment.

Tube-dwelling adult spionids were taken from the field and placed in sediment filled containers with different densities of A. rubrocincta (0, 160, or 320 individuals/m^2), in order to study spionid survival in sympatry with A. rubrocincta. The sediment used had the same grain size distribution described earlier. This natural sediment was untreated except for the removal of all tubiculous macrofauna at the start of the experiment. Each treatment density had five

replicates. All treatment containers were submerged in an unfiltered, running sea water bath for the duration of the experiment. Eight randomly chosen P. paucibranchiata, most of which had eggs in their tubes, were placed in each container after the A. rubrocincta had been added. After 1 mo the spionid tubes were collected, their condition noted, and the live inhabitants identified to species.

V. Spionid Predator Escape Responses

Six juvenile flatfish (*Parophrys vetulus*) and one juvenile sculpin (*Leptocottus armatus*) were placed with 20 tube-dwelling *Pseudopolydora paucibranchiata* in a large aquarium. The fish had been fed mussels, pieces of which were lying about in excess during the observations. The number of fish attacks and success rates on spionids were measured during 1 h observation periods on 2 consecutive days.

Results:

I. Axiothella rubrocincta Patch Characteristics and Individual Feeding Rates

A. rubrocincta patches are located in sediments of high sand, low silt-clay content (Fig. 2). Over 80% by weight of the mineral particles were less than 177 μm (2.5ϕ). Only 1.5% of the sediments were in the silt-clay range of less than 88 μm (3.5ϕ). A significant difference exists in % silt-clay abundance between A. rubrocincta Patches #1 and #2 ($p<0.05$, t-test). The % silt-clay in Patch #1 is greater than in other patches (Table 1).

Sand deposition experiments in the laboratory suggest that natural sand deposition would not invalidate the surface defecation mound count method used to estimate A. rubrocincta densities. The mean expired time for A. rubrocincta to produce new fecal mounds on the surface was 29 $\pm$ 4 hr (n=12), following consecutive 5 cm sand additions. Individuals took less time to reappear with each trial suggesting that field fecal mounds would still be visible if 15 cm of sediment were continously deposited over a 6 day period. This degree of deposition was not detected during the study at the field sites. Among all Lawson's Flat study sites, Johnson (1967) estimated a maximum change in sand height of 20 cm over 2 yr. In addition, erosion by natural wind and water currents pro-

bably did not invalidate the count method because partially exposed, yet intact tubes are visible where unconsolidated fecal mounds have been swept away.

A. Density within A. rubrocincta Patches

a. Patch Persistence

The three A. rubrocincta patches chosen for study in June 1975 were in existence in the same general locations in June 1977. Recent observations (January 1978) of the three Patches on Lawson's Flat demonstrate that they have persisted for at least 31 mo.

b. Changes in Density with Time

Mean monthly A. rubrocincta density was estimated in each patch from June 1975 to June 1976 and in December 1976, February 1977, and June 1977 (Fig. 3abc). Each "entire" patch was subdivided into an "upper" and "lower half" with respect to tidal height. The 95% confidence intervals about the mean densities are given in Table 2abc. A. rubrocincta densities of "entire" patches varied over time with June maxima and February minima in 1975-1976 (Fig. 3abc). The 1977 density estimates appear to repeat this trend. Results of comparisons of density estimates between sampling times are presented in Table 3. These comparisons are of two types: 1)densities of June vs.

February within years and 2)densities of the same month during different years. Type 1 comparisons demonstrate seasonal differences within years. For example, density significantly decreased within each of the three "entire" patches from June 1975 to February 1976 and from June 1976 to February 1977. Type 2 comparisons demonstrate similarities between years during given seasons. For example, there was no significant density change at any "entire" patch when comparing June 1975 to June 1976 or February 1976 to February 1977. The collective results of Type 1 and 2 comparisons indicate that A. rubrocincta densities fluctuated seasonally within all patches studied. However, comparison of June 1975 to June 1977 reveals a longterm significant decrease in density at all three "entire" patches.

c. Comparisons of Density "Between" Patches

Patch #1 is located at a lower tidal range than Patches #2 and #3. Although Patches #2 and #3 occupy similar tidal ranges, #2 is broadly separated from Patches #1 and #3 (Fig. 1). Comparisons were made among "entire" patches to assess the general significance of these location differences. Patch #1 ("entire") consistently had significantly greater density than Patches #2 and #3 ("entire") (Fig. 3, Table 4). No significant difference in density was found among all Patch #2 vs. Patch #3

("entire") comparisons, which span a 2 yr time period. The results indicate that tidal height, or some related factor, significantly affects A. rubrocincta density, whereas the broad separation of Patch #3 is not a significant factor.

In addition to the tidal range differences between "entire" patches, each patch regardless of its tidal range relative to other patches is considered to have an "upper" and "lower half" with respect to tidal height. Comparisons were made among the "upper" and among the "lower halves" of the patches to see if similarities in densities exist as the result of being the "upper" or "lower half" of an A. rubrocincta patch. The results indicate that similarities in density do not occur among "upper" or among "lower halves" of patches when the comparisons involve patches which are of different tidal heights (Table 4, "upper" and "lower"). For example, the comparison of the "upper half" of Patch #1 to that of #2 (non-overlapping tidal ranges) was consistently significantly different; whereas, the same comparison for Patch #2 and #3 (similar tidal ranges) consistently was not significantly different.

The results (Table 4) of "lower half" Patch #1 vs. #3 comparisons (non-overlapping tidal ranges) are an exception to the trend described above. No significant difference in A. rubrocincta was found among the patches for 3 of the 5 dates compared. Fig. 3abc demonstrates that Patches #2

and #3 consistently had higher A. rubrocincta density in the "lower half" of the patch. In contrast, the lower intertidal, Patch #1 had alternating higher density in the "upper" and "lower halves" depending upon the sampling time. Therefore, density changes in the "lower half" of Patch #1 caused it to be not significantly different than the "lower half" of Patch #3 at certain times. In general, the "upper" or "lower halves" of patches located at different tidal heights are significantly different.

B. Area of Axiothella rubrocincta Patches

Patch areas were estimated monthly from June 1975 to June 1976 and in December 1976, February 1977, and June 1977 (Fig. 4). Mean area of Patches #1, #2, and #3 over time was 958 m^2 (n=12), 587 m^2 (n=14), and 381 m^2 (n=14), respectively.

Perimeter maps of individual patches are presented in various combinations of the months- June 1975, 1976, 1977, September 1975, December 1975, 1976, February 1976, 1977, and March 1976. Maps from these dates, divided into two groups (A,B), provide information specific to A)the seasonal changes of A. rubrocincta populations from June 1975- 1977 (Fig. 5- 13), and to B)the community study conducted from June 1975- June 1976 (Fig. 14- 16).

Patch #1 did not change in shape or area over short periods of time (June 1975 vs. February 1976, December 1975 vs. 1976). Patch #1 area was greatest at the end of the study in June 1977. In comparison, Patches #2 and #3 changed area within years on a seasonal basis (e.g. February was the year's low area month during 1976 and 1977). Shrinkage of Patches #2 and #3 occurred from the lower density, upper intertidal areas. As in Patch #1, maximum area of #2 and #3 occurred in June 1977. There is a significant positive correlation ($r = +0.909$) of Patch #1 area with time. This correlation was not significant for Patches #2 and #3 due to seasonal (within year) area fluctuations (Fig. 4).

Monthly sampling (Group A, Fig. 5- 13) was more sensitive to the scale of seasonal change in patch area than trimonthly sampling (Group B, Fig. 14- 16). Group B maps indicate the perimeters of the A. rubrocincta patches during each of the five community sampling months. From this information, there is little evidence of change in shape or area at any patch (Fig. 14- 16). However, the Group A maps demonstrate the diminished area of Patches #2 and #3 during February 1976.

C. Interaction of Patch Area with Density

Regressions of density on area over all times were not significant for each of the patches. Pearson product-moment correlation coefficients between area and density were also not significant.

D. Individual Sediment Reworking Rates with respect to Tidal Height

There was no significant difference (ANOVA) among the mean weights of daily fecal mounds produced by individual A. rubrocincta living at the four experimental tidal heights (Table 5). I assume that sediment is drawn into worm tubes for deposit-feeding only during periods of tidal submergence. Because daily submergence times differed between tidal heights (Table 6), sediment reworking rates significantly increased (linear regression, $p<0.001$) with increasing tidal heights (Fig. 17).

II. The *Axiothella rubrocincta* Community

Polychaetes (16 species), crustaceans (15 species), and bivalves (8 species) were collected from within the patches and constitute *A. rubrocincta* macrofaunal communities (Table 7). Small numbers of fish, nematodes, oligochaetes, nemertians, and sipunculids were also collected.

The results indicate that certain species were "patch-specific". Other species which occurred in two patches were never collected in a third patch. *Pseudopolydora paucibranchiata* was rarely found within an *A. rubrocincta* patch and this occurred only at Patch #1 when it was collected. *Nebalia pugettensis*, *Aoroides columbiae*, and several Caridians were also limited to this mid-intertidal patch. All species found in Patches #2 and #3 were also found in Patch #1, which had the greatest species diversity (# of species). *Pygospio elegans*, *Paraphoxus epistomus*, and *Eohaustorius washingtonianus* were unique to Patch #2. Other species (*Macoma secta*, *Macoma nasuta*, *Polydora ligni*) never occurred in Patch #2, but were found in both #1 and #3.

Eleven common species or species groups were chosen for detailed analysis. Each analysis includes calculations of mean seasonal densities and two 3-way ANOVAs. All ANOVA significant main effects were statistically decom-

posed. In addition, significant ANOVA interactions were analyzed for the spionid polychaetes and venerid bivalves. A main purpose of the study was to determine which species or species groups were significantly more dense within or on the outer edges of A. rubrocincta patches (Main Effect C in the 3-way ANOVA). Table 8 summarizes the results, demonstrating that common surface-dwelling crustaceans, bivalves, and burrowing polychaetes were all more abundant within the patches. Spionid polychaetes were the only species group which was significantly less dense within A. rubrocincta patches.

A. Analysis of Individual Species or Groups

Corophium sp.

This group of filter-deposit feeding amphipods builds tubes in surface sediments. Mean seasonal densities and 95% confidence intervals are presented in Fig. 18 and Table 9.

I. 3-way ANOVA (Outside Left and Within Patches)

Main Effects:

All three of the main effects were significant (Table 10-I). No significant difference was found for the two a-priori among Study Site comparisons, although the Main Effect (A) was significant. Inspections of the group

sums among Study Sites and Fig. 18 indicate that Study Site (SS) #3 had significantly lower density. Student-Newman-Keuls (SNK) test comparisons were made to compare Corophium sp. densities among Sampling Times (Main Effect B). Few significant changes took place over time (as indicated by the high degree of connectance among Sampling Times on Table 10-I). June 1975 was not significantly different than the density of June 1976. Density was significantly greater in September 1975 than at all other Sampling Times. Corophium sp. density was significantly greater within the A. rubrocincta patches (Main Effect C). This is most clearly demonstrated at Study Site #2 (Fig. 18).

II. 3-way ANOVA (Outside Right and Within Patches)

Main Effects:

All main effects were significant (Table 10-II). SS #1 had significantly lower Corophium sp. densities than #2 and #3 (Main Effect A). Little change occurred in density through time, as indicated by the high degree of connectance between Sampling Times (Table 10-II, Main Effect B). However, densities significantly increased, especially at SS #3 (outside right of Patch #3), from June 1975 to June 1976. Corophium sp. density was maximal during September 1975 and June 1976. Density was significantly greater within A. rubrocincta patches (Main Effect C, Fig. 18).

Cumella vulgaris

This deposit feeding cumacean inhabits intertidal surface sediments. Mean seasonal densities and 95% confidence intervals are presented in Fig. 19 and Table 11.

I. 3-way ANOVA (Outside Left and Within Patches)

Main Effects:

All three of the main effects were significant (Table 12-I). Decomposition of Main Effect A (Study Sites) indicates that SS #1 had significantly higher C. vulgaris densities than #2 and #3. SS #2 had significantly lower densities than #1 and #3. Therefore, density was greatest at the lower intertidal Study Site and was strongly affected by which of the upper intertidal Study Sites (#2 or #3) it was estimated at. Few lines connect sampling times in the diagram (Table 12-I, Main Effect B) indicating seasonal density fluctuations. Density was significantly greater in June 1976 than in June 1975. C. vulgaris density was significantly greater within A. rubrocincta patches (Main Effect C). Fig. 19 demonstrates this relationship.

II. 3-way ANOVA (Outside Right and Within Patches)

Main Effects:

The ANOVA results (II) are the same as those of C. vulgaris ANOVA I.

Leptochelia dubia

This locally common tanaidacean lives in tubes, often among algae. It manipulates surface sediments while feeding. Mean seasonal densities and 95% confidence intervals are presented in Fig. 20 and Table 13.

I. 3-way ANOVA (Outside Left and Within Patches)

Main Effects:

All three of the main effects were significant (Table 14-I). Comparisons among Study Sites (Main Effect A) indicate significantly higher densities in SS #1, located lower in the intertidal. SS #2 had significantly lowest L. dubia density among Study Sites. Among Sampling Times (Main Effect B), June 1975 densities were lowest while those of March and June 1976 were highest. Density in June 1976 was significantly greater than in June 1975. L. dubia density was significantly greater within the A. rubrocincta patches (Main Effect C). This trend was most apparent in Patch #3 (Fig. 20). In contrast, L. dubia densities at SS #1 were often greater outside of the patch.

II. 3-way ANOVA (Outside Right and Within Patches)

Main Effects:

The ANOVA results (II) are the same as those of L. dubia ANOVA I.

Paraphoxus sp.

This deposit-filter feeder burrows in surface sands. It is one of the more common intertidal amphipods of the Bodega Bay region. Mean seasonal densities and 95% confidence intervals are presented in Fig. 21 and Table 15.

I. 3-way ANOVA (Outside Left and Within Patches)

Main Effects:

Two main effects were significant (Table 16-I). Among-patch comparisons (Main Effect A) indicate significantly higher Paraphoxus sp. densities at SS #2. Paraphoxus sp. density was significantly greater within the A. rubrocincta patches (Main Effect C).

II. 3-way ANOVA (Outside Right and Within Patches)

Main Effects:

Two main effects were significant (Table 16-II). No significant difference was found for the two a-priori comparisons, although the Main Effect A was significant. Inspection of the group sums among Study Sites and Fig. 21 indicate that SS #3 had significantly lower Paraphoxus sp. density. Paraphoxus sp. density was significantly greater within the A. rubrocincta patches (Main Effect C) (see Fig. 21).

Haploscoloplos elongatus

This deposit-feeding orbinid polychaete burrows in sands and muds. Mean seasonal densities and 95% confidence intervals are presented in Fig. 22 and Table 17.

I. 3-way ANOVA (Outside Left and Within Patches)

Main Effects:

The three main effects were highly significant (Table 18-I). Decomposition of Main Effect A (Study Sites) indicated that SS #1 had significantly lower H. elongatus densities than #2 and #3. Inspection of Fig. 22 indicates that densities were very high in SS #3 during the summer of 1975. SNK comparisons of Sampling Times (Main Effect B) demonstrate the significant decrease in density from June 1975 to December 1975, where it remained until community sampling was terminated in June 1976. H. elongatus density was significantly greater within the A. rubrocincta patches (Main Effect C).

II. 3-way ANOVA (Outside Right and Within Patches)

Main Effects:

The ANOVA results (II) are the same as those of H. elongatus ANOVA I.

Lumbrineris zonata

This deposit-feeding lumbrinerid polychaete burrows in sands and sandy muds. Mean seasonal densities and 95% confidence intervals are presented in Fig. 23 and Table 19.

I. 3-way ANOVA (Outside Left and Within Patches)

Main Effects:

Two main effects were significant (Table 20-I). Study Site #1 had significantly lower L. zonata densities than Study Sites #2 and #3 (Main Effect A). Comparisons among Sampling Times (Main Effect B) demonstrate that density was significantly lower in June 1976 than in June 1975. Significant differences between September 1975 and December 1975 indicate that the decrease occurred during those months (Fig. 23).

II. 3-way ANOVA (Outside Right and Within Patches)

Main Effects:

The ANOVA results (II) are the same as those of L. zonata ANOVA I. In addition, the Main Effect C was significant. L. zonata density was significantly greater within A. rubrocincta patches than on the outside (right) edges.

Burrowing Polychaetes

This group consists of combined data from at least six species of burrowers: Capitellids, Eteone sp., Haploscoloplos elongatus, Glycinde armiger, Lumbrineris zonata, and Nepthys caecoides. Mean seasonal densities and 95% confidence intervals are presented in Fig. 24 and Table 21.

I. 3-way ANOVA (Outside Left and Within Patches)

Main Effects:

The three main effects were significant (Table 22-I). No significant difference was found for the two a-priori among Study Site comparisons, although the Main Effect A was significant. Inspections of the group sums and Fig. 24 indicate that SS #3 had significantly higher Burrowing Polychaete density. SNK comparisons among Sampling Times (Main Effect B) demonstrate that density was significantly greater in June and September, 1975 than at any other time. Density was lowest in June 1976. Burrowing polychaete density was significantly greater within the A. rubrocincta patches (Main Effect C).

II. 3-way ANOVA (Outside Right and Within Patches)

Main Effects:

The ANOVA results (II) are the same as those of Burrowing Polychaetes ANOVA I. In addition, the a-priori comparison (Main Effect A) demonstrated that SS #2 had significantly lower Burrowing Polychaete density than #1, #3.

Spionid Polychaetes

These surface tube-builders deposit (and suspension) feed in muddy and sandy mud sediments. The following species of spionids were more abundant on the outer edges compared with samples taken from equivalent tidal heights within A. rubrocincta patches: Boccardia proboscidea Hartman, Polydora ligni Webster, Pseudopolydora kempi southern, Pseudopolydora paucibranchiata Okuda, Pygospio elegans Claparede, Rhynchospio arenicola Hartman, Spiophanes missionensis Hartman, and Streblospio benedicti Webster. The mean spionid densities estimated to the left of, to the right of, and within each of the three A. rubrocincta patches for each sampling time are presented in Fig. 25. The mean density outside of the patches was consistently greater than the "within patch" spionid density in 70% of the comparisons (n=30) of outside (left) vs. within and outside (right) vs. within. This trend was most consistent for Study Sites #2 and #3. The variances about the mean spionid densities are large and the 95% confidence intervals for each mean (n=6) are given in Table 23. Data were log transformed to better fulfill assumptions of ANOVA.

I. 3-way ANOVA (Outside Left and Within Patches)

Main Effects:

Two main effects were significant (Table 24-I). In

addition, the nesting which occurred among sets of replicates at each study site was significant. Significantly higher spionid densities occurred on the outside (left) of the A. rubrocincta patches (Main Effect C, Fig. 25). In order to determine which study sites had significantly different spionid densities (Main Effect A) two a-priori comparisons were performed. Study Site (SS) #1, located lowest in the intertidal zone, had significantly greater spionid density than the other SS. SS #2, which was broadly separated from the other sites, did not have a significantly different estimate of spionid density than that of other SS.

II. 3-way ANOVA (Outside Right and Within Patches)

Main Effects:

One of the main effects (C) and the nesting among sets of replicates within Study Sites were significant (Table 24-II). Significantly higher spionid densities were found outside of the A. rubrocincta patches (Fig. 25).

Interactions:

One first-order interaction (AxC) was significant. This indicates that estimated spionid densities from either the outside (right) or from within an A. rubrocincta patch (Main Effect C) were dependent upon the study site (Main Effect A) sampled. SS #1 had similar spionid densities within and outside of A. rubrocincta patches, while spionid densities at SS #2 and #3 decreased sharply within patches (Fig. 26).

Gemma gemma

This introduced bivalve filter feeds while in surface sand or sandy mud. Mean seasonal density and 95% confidence intervals are presented in Fig. 27 and Table 25.

I. 3-way ANOVA (Outside Left and Within Patches)

Main Effects:

All of the main effects were significant (Table 26-I). Comparisons among Study Sites (Main Effect A) demonstrated that SS #1 had significantly lower G. gemma densities than #2 and #3 (see Fig. 27). SNK comparisons indicate G. gemma's high rate of density change between Sampling Times (Main Effect B). Few lines connect sampling dates in the figure, thus demonstrating many significant differences. Densities were lowest in June 1975 and steadily rose to a June 1976 maximum. G. gemma density was significantly greater within A. rubrocincta patches (Main Effect C).

Interactions:

Three first order interactions, one second order interaction, and the nesting among sets of replicates were significant. Fig. 28 demonstrates the Study Site (A) x Sampling Time (B) interaction. Densities steadily increased over time at SS #2 and #3, but remained more constant at SS #1. Fig. 29 demonstrates the Study Site (A) x Sample Location within or outside of a patch (C) interaction. At SS #2 and #3 G. gemma densities were much greater within A. rubrocincta patches; whereas, densities were similar

irrespective of sample location at SS #1. Fig. 30 demonstrates the Sampling Time (B) x Sample Location (C) interaction. Within patches, G. gemma density steadily increased over time, whereas outside of the patches density was more constant. Fig. 31 a and b demonstrate the AxBxC interaction. Changes in G. gemma density at each Study Site (A) over Time (B) were different depending upon Sample Location (C) with respect to A. rubrocincta patches. Fig 31a and Fig. 31b separate "within patch" and"outside of patch" G. gemma data. The graphs (a and b) are similar for SS #1; however, density increased steadily "within patches" (Fig. 31a) and fluctuated outside of the patches (Fig. 31b) at SS #2 and SS #3.

II. 3-way ANOVA (Outside Right and Within Patches)

Main Effects:

The ANOVA results (II) are the same as those of G. gemma ANOVA I Main Effects.

Interactions:

Fig. 32 demonstrates the Study Site (A) x Sampling Time (B) interaction. G. gemma populations steadily increased over time at SS #2 and #3, but remained more constant at SS #1. Fig. 33 demonstrates the Study Site (A) Sample Location within or outside of an A. rubrocincta patch (C) interaction. At SS #2 and #3 G. gemma densities were much greater within A. rubrocincta patches, whereas

densities were similar irrespective of sample location at SS #1. Fig. 34 demonstrates the Sampling Time (B) x Sample Location (C) interaction. Within Patches, G. gemma density steadily increased over time, whereas outside of the patches density was more constant.

Transennella sp. (White Morph)

This burrowing venerid bivalve filter feeds at the sediment-water interface in sandy and sandy mud sediments. Mean seasonal densities and 95% confidence intervals are presented in Fig. 35 and Table 27.

I. 3-way ANOVA (Outside Left and Within Patches)

Main Effects:

Two main effects were significant (Table 28-I). Decomposition demonstrates that a)Study Site (SS) #1 had slightly lower densities than #2 and #3 and b)SS #2 had significantly higher Transennella sp. densities than SS #1 and #3 (Main Effect A). Transennella sp. density was significantly greater within A. rubrocincta patches (Effect C).

Interactions:

Three first order interactions and the nesting among sets of replicates within Study Sites were significant. Fig. 36 demonstrates the Study Site (A) x Sampling Time (B) interaction. Clam density at SS #2 and #3 fluctuated seasonally, with apparent September 1975 and June 1976 (Sampling Times #2,5) recruitment. Density at SS #2 increased from June 1975 to June 1976. Density at SS #1 decreased sharply from June to September 1975, when other Study Site densities were increasing. Density at SS #1 decreased slightly overall from June 1975 to June 1976. Fig. 37 demonstrates the Study Site (A) x Sample Location

(C) interaction. While Transennella sp. density increased greatly within patches at SS #2 and #3, densities were similar irrespective of sample location (C) at SS #1. Fig. 38 demonstrates the B x C interaction. Clam density within A. rubrocincta patches increased from June 1975 to June 1976, whereas, density decreased on outer edges.

II. 3-way ANOVA (Outside Right and Within Patches)

Main Effects:

All main effects were significant (Table 28-II). The ANOVA results (II) are the same as those of Transennella sp. ANOVA I Main Effects. In addition, June 1976 density was significantly greater than all other Sampling Times (Main Effect B). Density increased sharply within the patch at SS #2 at this time (see Fig. 35).

Interactions:

One first order interaction (Study Site x Sample Location with respect to A. rubrocincta patch) was significant (Fig. 39). While Transennella sp. density increased greatly within patches at SS #2 and #3, densities were similar irrespective of sample location at SS #1.

Transennella tantilla

This burrowing venerid bivalve filter feeds at the sediment-water interface in sandy and sandy mud sediments. Mean seasonal densities and 95% confidence intervals are presented in Fig. 40 and Table 29.

I. 3-way ANOVA (Outside Left and Within Patches)

Main Effects:

Two of the main effects were significant (Table 30-I). SNK comparison of densities in June 1975 and June 1976 (Main Effect B) demonstrates a significant decline with time. This trend is most apparent at SS #3 (Fig. 40). T. tantilla density was significantly greater within the A. rubrocincta patches (Main Effect C, Fig. 40).

Interactions:

Two first order interactions, one second order interaction, and the nesting among sets of replicates within Study Sites were significant. Fig. 41 demonstrates the Study Site (A) x Sampling Time (B) interaction. It appears that T. tantilla density decreased steadily over time at Study Sites (SS) #1 and #3. In contrast, density at SS #2 was low in June 1975 (Sampling Time #1), increased in December 1975 due to recruitment, and returned in June 1976 to a density similar to June 1975. The Study Site #2 population appeared to be stable from year to year with

seasonal fluctuations. Fig. 42 demonstrates the Sampling Time (B) x Sample Location (C) interaction. Within patches, T. tantilla density did not change greatly throughout the sampling period. In contrast, densities on the outside edges of patches declined drastically with time. Fig. 43 a and b demonstrates the significant AxBxC interaction. Changes in T. tantilla density at each SS (A) over Time (B) were different depending upon sample location within or outside of the A. rubrocincta patches (C). Fig. 43a and 43b separate within and outside of patch clam data. Within patches (Fig. 43a) clam densities at the three Study Sites fluctuated in different ways over time. Comparing June 1975 to June 1976, clam populations at SS #1, #2, and #3 increased, did not change, and decreased, respectively. In contrast, "outside of patch" clam density (Fig. 43b) decreased steadily at all Study Sites from June 1975 to June 1976.

II. 3-way ANOVA (Outside Right and Within Patches)

Main Effects:

Two main effects were significant (Table 30-II). Comparisons among Sampling Times (Main Effect B) indicate that June 1975 and June 1976 densities were not significantly different, although density had decreased with time. Densities increased significantly from September 1975 to December 1975 with recruitment to SS #2. From

December 1975 to March 1976 density decreased to its original (June 1975) level and remained through June 1976. T. tantilla density was significantly greater within the A. rubrocincta patches (Main Effect C).

Interactions:

One first order interaction and the nesting among sets of replicates within Study Sites were significant. Fig. 44 demonstrates the Study Site (Main Effect A) x Smpling Time (B) interaction. T. tantilla density at SS #1 and #2 fluctuated seasonally but returned to levels similar to June 1975 in June 1976. In contrast, clam density at SS #3 decreased from June 1975 to June 1976.

B. Correlations of Mean Density among Species of the *Axiothella rubrocincta* Community

All correlations were performed on species densities from "within" *A. rubrocincta* patch samples.

Cumella vulgaris and *Paraphoxus sp.*

A significant negative correlation ($r = -0.920$, $p<0.05$, $n=5$) was found between *Cumella vulgaris* (+1 log transformed) and *Paraphoxus sp.* density within Patch #3 through time. This relationship can be seen by comparing Fig. 19 with Fig. 21. Both species inhabit surface sediments and feed on organic matter within and on the substrate.

Venerid Bivalves

Gemma gemma and *Transennella sp.*

Data from Study Sites #1, #2, and #3 were pooled and a significant positive correlation ($r = +0.716$, $p<0.01$, $n=15$) was found between these species. Both sets of data were +1 log transformed. This was an expected result, as ANOVA demonstrated that the densities of both species were significantly lower at Study Site #1. However, the correlation of the two species' densities at Study Sites #2 and #3 only (where both occur in highest densities) was not significant ($r = +0.288$, ns, $n=10$). *Gemma gemma* and

Transennella sp. have similar shell size and shape.

Gemma gemma and Transennella tantilla

A significant negative correlation was found between these species at Study Sites #2 and #3 ($r= -0.652$, $p<0.05$, $n=10$). This relationship is also demonstrated by comparing Fig. 27 with Fig. 40.

Transennella sp. and Transennella tantilla

No significant correlation was found among the densities of these species. This may be the result of the strong G. gemma x Transennella tantilla interaction which occurred at this time at the upper intertidal study sites.

Spionid Polychaetes and Venerid Bivalves

Spionid Polychaetes and G. gemma

A significant negative correlation ($r= -0.831$, $p<0.01$, $n=15$) was found between these species groups. The data included all Study Sites. The G. gemma data was +1 log transformed. Other correlations between the spionid polychaetes and the two Transennella species were not significant. However, during a laboratory experiment (June 1977) a juvenile 20 mm long, T. tantilla was found in the gut of the spionid, Pseudopolydora paucibranchiata.

III. *A. rubrocincta* Resource Utilization and Substrate Modification

Approximately 17% (5 of 30 observations) of the time in the simulated sandflat, individuals were observed extending their heads and anterior segments 2-4 cm out of the tube oral aperture. These worms were selectively feeding on the reddish-brown OMA within and beyond the upper edge of the funnel. The feeding resulted in a distinct color change (reddish-brown to gray) in the surface sediment. Feeding ceased in an area once it had been thoroughly vacuumed. *A. rubrocincta* feeds in an area for approximately 40 days before switching to a new feeding location. Worms increased the switching rate to every 9 days when OMA were experimentally removed from the feeding funnels. Furthermore, experimental *A. rubrocincta* relocated their entire feeding apertures to areas of higher OMA content within 10 days following complete OMA removal. Worms in high OMA regions did not move during the experiment. Sieving of the experimental containers demonstrated that the bottoms of the *A. rubrocincta* tubes were branched. This condition is not common in nature but has been observed.

There exists an inverse relationship between *A. rubrocincta* density and OMA abundance (Fig. 45ab) which results from sediment reworking by *A. rubrocincta*. OMA can be separated

into two categories based upon compactness: 1)OMA_1 which are loosely bound (Fig. 46a), and 2)OMA_2 (Fig. 46b) which are tightly compacted. It appears that OMA_1 increased in abundance in the zero-A. rubrocincta density treatment (Fig. 45a) due to the removal of A. rubrocincta. This is readily seen by comparing OMA_1 values in experimental treatments with the field control. The significant treatment trends of Fig. 45, relating relative aggregate and mineral particle abundance to worm density, are given in Table 31. OMA_1 abundance decreased exponentially with linearly increasing A. rubrocincta density, with the greatest change in OMA_1 occurring at very low worm density (0-24 individuals/m^2) (Fig 45a). Loose aggregates were virtually nonexistent in those treatments with 72 or more A. rubrocincta/m^2. OMA_2 values remained constant and high at low A. rubrocincta densities, but decreased exponentially at high worm densities ($\geq 72/m^2$) (Fig. 45b). The depletion of most OMA at high worm densities resulted in clean sand composed of mineral particles (predominantly quartz, Fig. 46c) (Fig. 45c). On Lawson's Flat, mud occurs below and beside the more firm, sandy A. rubrocincta Patch #1, which ranges in tidal height from +0.0914 m to +0.2438 m, over a 16 m horizontal distance. Mud occurs along one edge of Patch #3 which is 70 m in length and ranges between +0.5486 m to +0.9144 m in tidal height.

IV. Spionid Resource Utilization and Interactions with *A. rubrocincta*

Gut contents of six *Pseudopolydora paucibranchiata* analyzed did not appear qualitatively different from the OMA_1 found on the nearby substrate or in the *A. rubrocincta* sediment modification analysis. Over 70% of the mineral particles extracted from both the gut contents and the field OMA_1 sample were $<16\ \mu m$ in length (Table 32).

Observations on the feeding behavior of *P. paucibranchiata* demonstrated that OMA was selectively chosen in all OMA densities. In substrates with virtually no OMA, individuals (n=10) increased the area searched by extending to greater than normal distances out of their tubes. This activity caused the prostomial region to be exposed, a position not normally assumed during feeding. In treatment substrates with large quantities of OMA_1, individuals (n=10) collected and drew the aggregates into their tubes solely with their palps. Occassionally worms piled or attached large pieces of OMA around their tubes. Other individuals within reach were seen taking these aggregates for themselves; however, no intraspecific aggressive encounters were observed. The result of these activities was a concentration of OMA around the *P. paucibranchiata* tubes, which left much of the substrate free of aggregates.

The anterior ends of all spionid tubes collected were predominantly composed of OMA. The mean lengths of mineral particles extracted from the two P. paucibranchiata tubes were 29 μm and 18 μm, approximately the size of mineral particles found within OMA_1 (see Table 32). A total of 25 spionid tubes of the following species were analyzed for the presence of OMA: B. proboscidea, P. ligni, P. kempi, P. paucibranchiata, P. elegans, and S. missionensis. Two main types of tubes were recognized, those occurring in muddy and those in sandy habitats. The exterior portion of tubes from muddy areas were composed of OMA_1. Tubes from sandy habitats consisted of mica, quartz and OMA. The inner sides of the tubes from all habitats were smooth from mucus secreted by the spionids.

Surface tube-building rate by P. paucibranchiata increased with OMA_1 relative abundance (Table 33). The fastest and least variable rates occurred in the pure OMA_1 (Table 33, S3; see Blake and Woodwick 1975 for a similar estimate). Building rates of spionids in A. rubrocincta patch substrates S1 and S2 differ markedly because of the addition of OMA_1 in S2. It was possible for individuals to build tubes in the pure A. rubrocincta patch sediment (S1), though at a very slow rate. These individuals were seen collecting the scarce OMA and incorporating it into their tubes along with mineral particles. S2 individuals

were observed to selectively gather OMA and to reject the heavier mineral particles. Quartz, mica, and shell fragments were channelled in with the palps, but were usually rejected at the prostomium.

Spionid survival was inversely related to A. rubrocincta density (Table 34). After 4 wk, 80% (8 of 10) of the samples containing A. rubrocincta had less than the initial sympatric spionid density (8); the majority (5 of 8 samples) had ≤ 3 worms remaining. Blackened and decomposing spionid tubes were found in all of the samples containing A. rubrocincta, although none were found in any of the control samples. It was not possible to distinguish P. paucibranchiata recruits from the original adults because of the rapid growth rates of the newly settled juveniles (see Blake and Woodwick 1975). It can be seen that spionid larval settlement was significantly greater when no A. rubrocincta was present, by taking into account the original number of spionid adults. P. kempi larvae, all of which entered the experimental system via the sea water inlet, had significantly greater ($p<0.05$, t-test) settlement when A. rubrocincta was not present.

V. Spionid Predator Escape Responses

Fish attacked only those spionids (*Pseudopolydora paucibranchiata*) which exposed their palps during feeding. The spionids withdrew rapidly into their tubes when touched suddenly by attacking fish and when swimming fish created currents nearby. In the aquarium, the flatfish (*Parophrys vetulus*) made 21 attacks on the spionids. All of the attacks were unsuccessful. *P. vetulus* attacked by aiming for the palp junction at the top of the worm's tube. Attacked spionids remained in their tubes for periods of 2-30 minutes before resuming feeding. The sculpin (*Leptocottus armatus*) did not attack the spionids. The flatfish have narrow "picker" mouths, while the mouth of the sculpin is broad. Both species of fish occur at the study sites.

Discussion:

I. Axiothella rubrocincta Patch Characteristics and Individual Feeding Rates

The three A. rubrocincta patches chosen for a population and community analysis persisted from June 1975 for at least 31 months. The study area on Lawson's Flat appears to be physically stable over time, relative to Dillon or Salmon Creek Beaches, permitting this persistance. Several hypotheses have been suggested to explain the occurrence of dense patches in nature (see Pianka 1974). These hypotheses, which primarily involve predator defense and reproductive efficiency, have not been tested in this study.

A. rubrocincta densities within patches varied significantly over time (1975, 1976, 1977). Density changes were seasonal with June maxima and February minima. Although these trends are supported by data, I feel that particularly windy days could significantly alter the accuracy of the sampling method. The process (e.g. recruitment, mortality, migration) by which the density change occurred is not known; however, the absence of A. rubrocincta juveniles in community cores and the experimental data concerning individual movement indicate that migration may be important. Total area of the upper intertidal patches (#2 and #3) also changed seasonally. However,

"within patch" density and area of individual patches were not significantly correlated over time. A significant negative correlation would have been expected if individual migration were the only cause of the changes in"within patch" density. A significant positive correlation would have indicated recruitment accompanied by patch growth. The nonsignificant correlation may indicate a true lack of association or be the result of confounding recruitment-mortality-migration interactions.

It was shown in the field experiment (conducted at Patches #1 and #3) that individual feeding rates decreased as tidal height position decreased. The result indicates that individuals living at higher tidal heights increased their sediment reworking rates in order to compensate for prolonged exposure times. Body size and food availability are also significant variables affecting this rate (see Kudenov 1971).

II. The *Axiothella rubrocincta* Community

Due to surface destabilization and space occupation by *A. rubrocincta* it was initially hypothesized that most species would be less dense within the patches. However, ten of eleven common species and species groups were found to be significantly more dense within *A. rubrocincta* patches. These groups do not share a common feeding method or depth position in the sediment. This suggests that several structuring mechanisms may be important in determining the distribution of these species and species groups.

Rhoads and Young (1970) hypothesized that filter-feeders should inhabit sandy areas in order to 1)prevent clogging of filtering structures and 2)avoid potentially predatory and burying deposit-feeders. The hypothesis assumed that deposit feeders were restricted to silty areas, due to a lack of food elsewhere. In the present study, several species of filter-feeders (e.g. *Corophium sp.*, *Paraphoxus sp.*, venerid bivalves) were more dense within the sandy *A. rubrocincta* patches as predicted by the first half of the hypothesis. Although *A. rubrocincta* is a deposit-feeder, it is not restricted to silty areas, and is supplied with sufficient food in the sandy areas of Lawson's Flat. Consequently, in contradiction to the second half of Rhoads and Young's hypothesis, filter feeders were

found to be more dense in sympatry with a deposit feeder. The degree to which A. rubrocincta ingests and buries filter feeders has not been measured. I have observed the "passing alive" of juvenile Transenmella tantilla through the tube of feeding A. rubrocincta. The ecological significance of predation on larvae and their passing alive is poorly understood, but has been treated by Mileikovsky (1974).

Burrowing polychaetes were also significantly more dense within the A. rubrocincta patches. Woodin (1974) hypothesized and provided evidence that burrowing polychaetes were inferior to tube-builders in competition for space. Adult A. rubrocincta densities on Lawson's Flat were much lower than the juvenile densities reported by Woodin in her paper. Either the results of the present study contradict Woodin's competition hypothesis or densities were not high enough to create space limitation. Factors which produced the observed burrowing polychaete distribution have not been determined.

Significant interspecific density correlations were found among species collected in the community samples. The densities of two small surface-dwelling crustaceans (Paraphoxus sp. and Cumella vulgaris) were negatively correlated through time at Patch #3. The nature of the interaction has not been determined. In addition, densities

of venerid bivalves were correlated through time. At Study Sites #2 and #3, where the highest densities of G. gemma and Transennella sp. occurred, their densities were not correlated. However, their densities were positively correlated when considering all Study Sites. Both species had significantly lower densities at Study Site #1. Ecological factors (physical and biological) are likely to be different at Study Site #1 because it is at a much lower tidal height. This correlational result indicates that the densities of the two species changed in a similar fashion in response to these tidal height related variables. However, within the more narrow intertidal range were the two species coexisted in high densities, changes in their population sizes were not positively correlated.

G. gemma density was significantly negatively correlated with that of Transennella tantilla at Study Sites #2 and #3. As indicated by ANOVA, G. gemma density steadily increased throughout the sampling period within Study Sites #2 and #3 (Fig. 31a). T. tantilla density significantly decreased over time, particularly at SS #3. G. gemma replaced T. tantilla at SS #3 during the sampling period (June 1975- June 1976). Several nonquantatative samples were recently (March 1978) collected and examined from SS #3. Both venerid species were abundant in the

samples. Therefore, one year of community sampling was insufficient and potentially misleading in documenting interspecific density correlations.

Densities of spionid polychaetes were negatively correlated with G. gemma densities. Results of ANOVA demonstrated that among the common species collected within and around A. rubrocincta patches, spionid polychaetes were unique in being more dense on the outside edges of the patches (Table 8). However, among "within A. rubrocincta patch" samples significantly more spionids were found at Study Site #1 (Fig. 26). The spionid-G. gemma correlation is understandable because, in contrast to the spionids, G. gemma density was significantly greater within A. rubrocincta patches (Table 8) and significantly less dense at Study Site #1 (Table 26). The negative spionid-G. gemma interaction is possibly mediated by A. rubrocincta. Spionids and G. gemma are surface feeders. Spionids differ from venerid bivalves ecologically in their tube requirement. Interactions between these species are currently being investigated.

III. *Axiothella rubrocincta* Resource Utilization and Substrate Modification

The experimental data suggest that the observed habitat segregation between *A. rubrocincta* and spionid polychaetes is biologically induced. The over-dispersed pattern is not likely to be the sole result of physical factors since the pattern is clearly found at Study Sites #2 and #3 which are broadly separated on the sandflat but of similar tidal height (Fig. 25, Fig. 1). Spionid segregation from *A. rubrocincta* Patch #1, located lower in the intertidal, is less pronounced than at other patches (Fig. 25). This result suggests that, among study sites, physical differences (e.g. productivity) due to tidal height affect the degree to which spionids are excluded from *A. rubrocincta* patches. However, within a tidal range, physical differences arising from the separation of study locations on the sandflat do not appear to alter the biologically induced *A. rubrocincta*-spionid segregation.

The concept that substrate modification by deposit feeders may have a significant effect on the biological community is not new (Sanders 1960, Sanders et al. 1962, Johnson 1964, Fager 1964, Gordon 1966, Rhoads and Young 1970, Myers 1977a and 1977b). In this study, feeding, tube-building, and survival of spionid polychaetes were found to be significantly affected by substrate modifications

caused by A. rubrocincta. Substrate characteristics are of prime importance in understanding the A. rubrocincta-spionid interactions.

In this study two methods were used to analyze substrates: 1)dry sieving of mineral particles and 2) individual description of both stained mineral particles and OMA, following PAS staining. The dry sieving method provides accurate information on mineral particle sizes. However, this technique destroys the organic matrices which aggregate many of the clay and silt sized particles (OMA) in nature. Because of the composition of OMA, its abundance has been shown to be positively related to the percent organic carbon and the abundance of silt-clay fractions in sediments (Gallucci and Hylleberg 1977, Johnson 1977). In this study, the assumption is made that the magnitude of the silt-clay fraction is positively related with natural OMA abundance. The data indicate that A. rubrocincta Patch #1, which was lowest in the intertidal zone, had the highest resource (OMA) availability among patches (Table 1). This apparent productivity difference may explain why Patch #1 also had the highest A. rubrocincta and spionid densities among "inside of patch" samples (Table 1, Fig. 26). Significantly higher spionid densities were estimated at SS #1 than at Sites #2 and #3 (Table 24, a priori comparison).

The second method of sediment analysis was used to study the substrate modifications resulting from A.

rubrocincta feeding. The most obvious compositional modification was the inverse relationship between OMA abundance on the substrate surface and A. rubrocincta density (Fig. 45). Feeding by A. rubrocincta resulted in a clean, sandy substrate dominated by mineral particles and containing little OMA. The correspondence between substrate type (sand or mud) and the presence or absence of A. rubrocincta in the field represents strong indirect evidence that A. rubrocincta deposit feeding significantly modifies natural sediment composition. In a study of the effects of deposit feeders on suspension feeders, Rhoads and Young (1970) found that, unlike stations dominated by deposit feeding bivalves, stations dominated by tubiculous deposit-feeding polychaetes were sandy in texture and of low organic content. The possibility that the Atlantic coast polychaetes had modified the substrate in a manner similar to A. rubrocincta on Lawson's Flat, was not reported.

By experimentally studying A. rubrocincta feeding behavior, the mechanisms by which it modifies substrates were determined. A. rubrocincta depletes the OMA supplies within substrates by direct ingestion and by constantly reworking the substrate surface. Reworking may cause a physical breakdown and the removal of the aggregates from the area by currents. It appears that A. rubrocincta has three feeding habits: 1)feeding on organic matter

and encrusted sand particles in the funnel while the animal remains in the tube, 2)selectively feeding on the surface OMA by extending the body from the tube and 3)relocating the feeding aperture to a new location. The first habit, though safe, requires a sufficiently high renewal rate of food in the immediate environment. Surface deposit-feeding (Habit #2) (also described by Kudenov 1971) is unique because A. rubrocincta lacks palps or tentacles which are present on most surface deposit-feeding species. This habit enhances food gathering ability because it is coordinated and selects OMA. However, this behavior increases the probability of injury or death by vertebrate and invertebrate predators. A. rubrocincta is a prey item to common shorebirds such as the short-billed, visually feeding Black-bellied Plover (Pluvialis squaterola), the Dunlin (Calidris alpina), and the Marbled Godwit (Limosa fedoa) (Page and Stenzel 1975).

By assuming that: a)A. rubrocincta always selects OMA when available because it is the richest food source and b)predator induced A. rubrocincta mortality is low, one could predict Habit #2 to be more common in areas of higher OMA content. For a given amount of organic material, the weight of mineral particles (Habit #1 food source) is greater than OMA (Habit #2 food source). Therefore, differences in the weights of sediment defecation mounds could indicate different feeding habits among individual worms

(note - this has not been tested). This simplified model predicts that defecation mound weights at Patch #1, which was OMA rich compared to the higher intertidal patches (Table 1), should be significantly less than those of Patches #2 and #3. However, field data do not support the model's predictions. The ANOVA result of the field sediment reworking rate experiment (Table 5) indicates that mound weights were not significantly different across the intertidal zone (through Patches #1 and #3). If the model is made more complex to include significant predator induced A. rubrocincta mortality, it would then predict that although OMA are available on the surface for selective feeding (Habit #2), they would rarely be eaten due to the risk of predation. These individuals would primarily feed on mineral particles from within the tube (Habit #1), just as those living in OMA sparse areas (i.e. upper intertidal patches). If in fact the field data can be used as a feeding habit indicator, then those data support the "predation" model. Differences in the intensity of bird predation among the three A. rubrocincta patches is likely to be a function of the amount of time that shallow water (≤ 5 cm) covers the patches. This aspect of the A. rubrocincta study is currently under investigation.

Individual A. rubrocincta that relocate their feeding apertures (Habit #3) during periods of low OMA abundance expend energy in tube-building. This behavior took place

regularly in the simulated sandflat and increased in frequency following experimental reduction of OMA. Individuals may migrate through branching in the tube as this condition has been observed in nature and in the laboratory. Small changes in patch shapes over time (Fig. 5-16) may be the result of this behavior in nature. These data on A. rubrocincta feeding habits do not demonstrate that OMA is limited in nature, but they clearly show that during periods of normal and low OMA abundance feeding individuals incur risks and energy expenditures to obtain it. The data collectively suggest that OMA is an important food source to A. rubrocincta.

IV. Spionid Resource Utilization and Interactions with *Axiothella rubrocincta*

The results from laboratory and field data demonstrate that spionids are very dependent upon OMA for food and tube-building material. Gut contents of *Pseudopolydora paucibranchiata* (Spionidae) contained only OMA, and OMA feeding selectivity was observed in a variety of laboratory experiments. Furthermore, *P. paucibranchiata* radically changed its feeding behavior when OMA was not abundant. The modified feeding behavior included hyperextension of feeding palps away from the tube aperture in order to increase the foraging area. Foraging strategies of ants change in a similar manner when food density is low (Bernstein 1975). This spionid feeding modification caused the cephalic region to be exposed, increasing the probability of a successful attack by a predator. Furthermore, laboratory experiments indicate that *P. paucibranchiata* can construct tubes six times faster in sediment from *A. rubrocincta* patches to which OMA are added. This increased tube-building efficiency is probably due to the use of light OMA particles which are easier to manipulate than mineral grains.

In the absence of potential bird and fish predators, the survival of adult (*P. paucibranchiata*) and larval (*P. paucibranchiata* and *P. kempi*) spionids was very low

in substrates containing high A. rubrocincta densities. Survival was high in substrates devoid of A. rubrocincta (Table 34). Many of the adult spionids sympatric with A. rubrocincta died within their tubes, as indicated by their blackened, decomposed state. Spionid larvae were unsuccessful in colonizing substrates containing A. rubrocincta possibly because they found these areas unsuitable and delayed settlement or they settled and subsequently died due to A. rubrocincta. Potential sources of larval spionid mortality caused by A. rubrocincta include OMA depletion, surface instability of the substrate and predation. Regardless of how the spionid larvae behaved, this experimental result emphasizes the importance of successful larval settlement in determining the adult distribution. This experimental result is in agreement with the adult-larval interaction hypothesis which states that "the maintenance of these discrete dense assemblages in infaunal systems is due to interactions among the established infaunal individuals and settling larvae"(Woodin 1976). This hypothesis and the experimental result, while pinpointing the life-stage at which adult dispersion patterns may be formed, do not identify or describe the selective forces which structure infaunal communities.

This study's results collectively indicate that interspecific competition for OMA is an important selective force determining the adult spionid distribution pattern.

Deposit-feeding A. rubrocincta are capable of depleting OMA even at low worm densities (Fig. 45), while natural A. rubrocincta densities are usually much higher (Table 1). Spionids require OMA for food and tube material, and thus have lower fitness when sympatric with A. rubrocincta when OMA is limited. The results also indicate that "among study sites", #1 had the highest environmental productivity (OMA abundance) (Table 1). In contrast to higher intertidal Study Sites #2 and #3, spionid density was often as high within the A. rubrocincta patch as on the outside (Fig. 25, Fig. 26). This indicates that the intensity of competition is not as great at A. rubrocincta Patch #1, where OMA is abundant, as at the less productive patches.

The intensity of a competitive interaction may be lessened by alternative outcomes such as segregation by habitat, food-type, and feeding times (Schoener 1974a). Levinton (1972, 1977) has hypothesized and provided evidence that interspecific competition for food between deposit-feeders commonly occurs in temperate soft-substrate communities. Substrate resource utilization by the family Spionidae on Lawson's Flat is included within that of A. rubrocincta, although there exist between-species (spionids) differences (Robert Whitlatch, personal communication). The experimental results show that A. rubrocincta and spionids

feed on surface organic-mineral aggregates (OMA) ("specialists"), while A. rubrocincta also feeds nonselectively on a wide range of nutritious sediments ("generalist") (see Kudenov 1971). The "included niche" phenomenon can theoretically exist if the included species has a sufficiently high feeding efficiency (Schoener 1974b). However, most spionids do not coexist with A. rubrocincta on Lawson's Flat. "Specialist" strategies are successful only when the resource availability is predictable and sufficiently high (Levins 1968). The data indicate that the OMA availability for spionids within A. rubrocincta Patches #2 and #3 does not meet these requirements. Spionids and A. rubrocincta have high diet overlap but low habitat overlap, a condition found for competing species of birds, lizards, fish, and crustaceans (Schoener 1974a).

V. Spionid Predator Escape Responses

Little data is available to determine the effect of predation on the adult spionid distribution. However, its potential for structuring this community should not be overlooked (see Dayton 1971, Sprules 1972, Zaret and Kerfoot 1975, Goss-Custard 1977, Vance 1977). For example, A. rubrocincta may ingest settling spionid larvae. Because A. rubrocincta often lives in high densities, this could effectively exclude spionids from those areas. Furthermore, common shorebirds such as the Marbled Godwit (Limosa fedoa), the Dunlin (C. alpina) and the Short-billed Dowitcher (Limnodromus griseus) are spionid predators (Page and Stenzel 1975). Visually feeding, predatory juvenile flatfish are attracted by the waving of palps, an obligatory movement of spionids when feeding. Laboratory results indicate that when OMA is not limited, spionids extend only their palps in feeding, and can withdraw them without injury during a flatfish attack. However, when OMA is limited, spionids modify their feeding behavior, reducing the effective predation defense of minimizing body exposure. Therefore, if a spionid was to be eaten by a visual predator under these circumstances (OMA limited), interspecific competition with A. rubrocincta for OMA would be the ultimate selective mechanism, although predation would be the direct cause of death.

Summary:

The synecology of Axiothella rubrocincta patches was investigated. Patches were persistent through time with seasonal area-density fluctuations. Individual migration may explain these fluctuations. Although A. rubrocincta forms dense patches which occupy space and create an unstable surface, ten of eleven of the most common species or species groups were found to be more dense within the patches than on the outer edges. The densities of several ecologically similar species within the patches were correlated through time, however the degree to which A. rubrocincta mediated the correlations was not determined.

Interspecific competition between A. rubrocincta and spionids for a limited supply of OMA was established as a primary interspecies interaction accounting for the observed pattern of habitat segregation. This segregation is more pronounced in less productive habitats. This study suggests that this interaction primarily operates on settling larval spionids, preventing successful larval colonization of substrates inhabited by A. rubrocincta. While the larval life-stage is critical in establishing the adult distribution pattern, interspecific competition between mature adults is equally severe. Spionids inhabiting A. rubrocincta patches where OMA is limited expend more time and energy obtaining food and tube materials relative to individual spionids

on the outer edges of A. rubrocincta patches. In addition, "within A. rubrocincta patch" spionids are likely to be more exposed to visual predators while searching for food.

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Table Legend

Table Page

	Axiothella Patch #								
	1			2			3		
	$\bar{X}$	S	N	$\bar{X}$	S	N	$\bar{X}$	S	N
% SILT-CLAY	2.45	0.64	2	0.45	0.21	2	1.30	0.14	2
AREA (M^2)	911.25	63.81	4	601.20	74.63	5	405.00	43.63	5
DENSITY (M^2)									
JUNE 1975	103.00	93.32	117	36.32	46.68	73	34.36	30.24	69
SEPT 1975	—	—	—	26.00	31.24	105	16.88	17.60	65
DEC 1975	47.12	43.12	112	22.40	27.04	80	19.88	20.12	68
MAR 1976	66.40	63.08	40	22.92	28.04	40	31.72	43.40	40
JUNE 1976	86.40	69.40	40	25.12	31.04	40	37.40	43.36	37

TABLE 1

AXIOTHELLA RUBROCINCTA PATCH # 1

SAMPLE DATE	UPPER HALF		LOWER HALF		ENTIRE	
	C.I.	n	C.I.	n	C.I.	n
1975						
JU	6.17	54	6.06	63	4.27	117
JL	3.58	51	4.08	56	2.71	107
AG	5.32	60	5.32	62	3.43	122
SP	--	--	--	--	--	--
OC	--	--	--	--	--	--
NV	--	--	--	--	--	--
DC	3.06	52	2.76	60	2.03	112
1976						
JA	--	--	--	--	--	--
FB	2.63	57	3.53	65	2.23	122
MR	5.89	20	8.59	20	5.04	40
AP	8.61	20	6.55	20	5.24	40
MY	6.68	20	7.80	20	4.91	40
JU	8.87	20	7.21	20	5.54	40
DC	6.63	20	9.30	20	5.50	40
1977						
FB	7.81	20	4.37	20	4.40	40
JU	10.53	20	3.31	20	6.00	40

TABLE 2a. 95% CONFIDENCE INTERVALS (C.I.) ABOUT THE MEAN A. RUBROCINCTA DENSITIES (Fig. 3 abc) over TIME. THE ENTIRE PATCH HAS BEEN SUBDIVIDED INTO UPPER AND LOWER HALVES. n= SAMPLE SIZE.

AXIOTHELLA RUBROCINCTA PATCH #2

SAMPLE DATE	UPPER HALF		LOWER HALF		ENTIRE	
	C.I.	n	C.I.	n	C.I.	n
1975						
JU	0.54	27	3.89	46	2.73	73
JL	0.41	33	3.59	52	2.56	85
AG	0.35	27	2.05	55	1.53	82
SP	0.38	40	2.19	65	1.52	105
OC	0.40	55	1.92	50	1.53	105
NV	--	--	--	--	--	--
DC	0.29	32	2.26	48	1.50	80
1976						
JA	--	--	--	--	--	--
FB	0.55	19	1.25	37	0.95	56
MR	0.40	20	3.55	20	2.24	40
AP	0.60	20	3.01	20	1.85	40
MY	0.73	20	3.83	20	2.38	40
JU	0.61	20	4.06	20	2.48	40
DC	1.16	20	1.55	20	0.98	40
1977						
FB	0.17	20	1.05	20	0.56	40
JU	2.06	20	3.33	20	1.99	40

TABLE 2b.

AXIOTHELLA RUBROCINCTA PATCH #3

SAMPLE DATE	UPPER HALF		LOWER HALF		ENTIRE	
	C.I.	n	C.I.	n	C.I.	n
1975						
JU	1.84	25	2.57	44	1.82	69
JL	1.51	27	2.37	43	1.68	70
AG	1.25	20	1.94	44	1.47	64
SP	1.01	21	1.49	44	1.09	65
OC	0.49	30	1.77	51	1.27	81
NV	--	--	--	--	--	--
DC	0.85	26	1.73	42	1.22	68
1976						
JA	--	--	--	--	--	--
FB	1.73	12	1.61	28	1.20	40
MR	2.11	20	5.75	20	3.47	40
AP	0.33	08	4.00	20	2.55	28
MY	0.35	17	3.26	20	1.89	37
JU	0.25	17	4.94	20	3.60	37
DC	0.45	08	2.25	20	1.90	28
1977						
FB	5.67	06	0.57	20	2.13	26
JU	1.03	18	4.22	20	2.41	38

TABLE 2c.

TYPE	SAMPLE DATES COMPARED	ENTIRE PATCHES 1	2	3
1	JU '75 vs. FB '76	0.001 (↓)	0.001 (↓)	0.001 (↓)
1	JU '76 vs. FB '77	0.001 (↓)	0.01 (↓)	0.05 (↓)
1	FB '77 vs. JU '77	ns	0.001 (↑)	ns
2	JU '75 vs. JU '76	ns	ns	ns
2	FB '76 vs. FB '77	ns	ns	ns
2	JU '75 vs. JU '77	0.01 (↓)	0.05 (↓)	0.001 (↓)
		LOWER HALVES OF PATCHES		
		1	2	3
1	JU '75 vs. FB '76	0.01 (↓)	0.001 (↓)	0.01 (↓)
1	JU '76 vs. FB '77	0.05 (↓)	0.001 (↓)	0.001 (↓)
1	FB '77 vs. JU '77	ns	0.05 (↑)	ns
2	JU '75 vs. JU '76	ns	ns	0.05 (↑)
2	FB '76 vs. FB '77	ns	0.05 (↓)	ns
2	JU '75 vs. JU '77	0.01 (↓)	0.01 (↓)	ns
		UPPER HALVES OF PATCHES		
		1	2	3
1	JU '75 vs. FB '76	0.01 (↓)	0.01 (↓)	0.001 (↓)
1	JU '76 vs. FB '77	0.01 (↓)	ns	ns
1	FB '77 vs. JU '77	ns	0.001 (↑)	0.05 (↑)
2	JU '75 vs. JU '76	ns	ns	0.001 (↓)
2	FB '76 vs. FB '77	ns	ns	ns
2	JU '75 vs. JU '77	ns	ns	0.05 (↓)

TABLE 3. BETWEEN SAMPLING TIMES COMPARISONS OF A. RUBROCINCTA DENSITY AT # PATCHES. ENTIRE PATCHES HAVE BEEN DIVIDED INTO UPPER AND LOWER HALVES. LEVEL OF SIGNIFICANCE IS GIVEN; ns= NOT SIGNIFICANTLY DIFFERENT; ARROWS INDICATE THE TYPE OF DENSITY CHANGE OVER SPECIFIED TIMES. WILCOXON 2-SAMPLE TEST. SEE TEXT FOR MEANING OF "TYPE" OF COMPARISON.

	SAMPLE DATE				
	JU '75	FB '76	JU '76	FB '77	JU '77
IRE PATCH					
vs. 2	0.001 (1>2)	0.001 (1>2)	0.001 (1>2)	0.001 (1>2)	0.001 (1>2)
vs. 3	ns	ns	ns	ns	ns
vs. 3	0.001 (1>3)	0.001 (1>3)	0.001 (1>3)	0.01 (1>3)	0.01 (1>3)
ER HALF					
vs. 2	0.001 (1>2)	0.01 (1>2)	0.05 (1>2)	0.001 (1>2)	ns
vs. 3	ns	ns	ns	0.05 (3>2)	ns
vs. 3	0.01 (1>3)	0.01 (1>3)	ns	ns	ns
ER HALF					
vs. 2	0.001 (1>2)	0.001 (1>2)	0.001 (1>2)	0.001 (1>2)	0.001 (1>2)
vs. 3	ns	ns	ns	ns	ns
vs. 3	0.001 (1>3)	0.001 (1>3)	0.001 (1>3)	0.001 (1>3)	0.001 (1>3)

TABLE 4. BETWEEN PATCH COMPARISONS OF A. RUBROCINCTA DENSITY AT 5 TIMES. LEVEL OF SIGNIFICANCE IS GIVEN; ns= NOT SIGNIFICANTLY DIFFERENT; NUMBERS IN ( ) INDICATE WHICH PATCH WAS SIGNIFICANTLY GREATER. WILCOXON 2-SAMPLE TEST.

TIDAL HEIGHT (m)	INDIVIDUAL	MEAN WEIGHT(g) OF DAILY FECAL MOUNDS	n(DAYS)
1.128			
	1	14.8	4
	2	12.3	7
	3	6.4	7
	4	6.5	4
	5	4.7	5
0.914			
	1	12.0	7
	2	11.1	6
	3	7.2	7
	4	6.1	7
	5	3.6	2
0.716			
	1	12.1	7
	2	9.8	6
	3	8.5	6
	4	7.9	7
	5	5.9	7
0.640			
	1	12.6	7
	2	9.2	4
	3	9.2	2
	4	9.1	7
	5	5.6	2

TABLE 5. SEDIMENT REWORKING BY A. RUBROCINCTA AT 4 TIDAL HEIGHTS ON LAWSON'S FLAT. REPEATED DAILY COLLECTIONS OF THE SAME INDIVIDUAL'S FECAL MOUNDS WERE MADE FOR UP TO 7 DAYS. SEPTEMBER 18-24, 1975.

TIDAL HEIGHT (m)	DAY #						
	1	2	3	4	5	6	7
1.128	39	38	38	33	34	35	32
0.914	56	54	55	50	51	51	49
0.716	71	71	70	64	66	67	64
0.640	77	76	76	75	72	72	76

TABLE 6. THE % SUBMERGENCE TIME PER DAY (SEPTEMBER 18-24, 1975) AT 4 TIDAL HEIGHTS ON LAWSON'S FLAT. DATA USED TO CALCULATE SEDIMENT REWORKING RATES.

Crustacea (Arthropoda)

* Cumella vulgaris 123
* Leptochelia dubia 123
* Phoxocephalidae 123
  Paraphoxus milleri 123
  Paraphoxus epistomus 2
  Paraphoxus tridentatus 123
* Corophiidae 123
  Corophium acherusicum-insidiosum-uenoi 123
  Corophium brevis 12
  Ampithoe valida 123
  Allorchestes angusta 123
  Aoroides columbiae 1
  Eohaustorius washingtonianus 2
  Nebalia pugettensis 1
  Crangon franciscorum 1
  Hemigrapsus oregonensis 1
  Heptacarpus paludicola 1

Bivalvia (Mollusca)

* Gemma gemma 123
* Transennella tantilla (brown) 123
* Transennella sp. (white morph) 123
  Macoma nasuta 13
  Macoma secta 13
  Lyonsia californica 1
  Protothaca staminea 13
  Tellina nuculoides 3

Polychaetes (Annelida)

* Burrowing Polychaetes 123
* Haploscoloplos elongatus 123
* Lumbrineris zonata 123
  Eteone californica 123
  Capitellidae 123
  Glycinde armigera 123
  Nephtys caecoides 123
* Spionid Polychaetes 123
  Polydora ligni 13
  Pseudopolydora kempi 13
  Pseudopolydora paucibranchiata 1
  Pygospio elegans 2
  Capitella capitata 13
  Mediomastus californiensis 123
  Notomastus tenuis 13
  Anaitides williamsi 1
  Magelona pitelkai 1
  Platynereis bicanaliculata 123
  Pista pacifica 1

TABLE 7.

LIST OF SPECIES AND SPECIES GROUPS COLLECTED FROM WITHIN A.RUBROCINCTA PATCHES (INDICATED BY THE # 's). * - INDICATES THAT MEAN DENSITIES AND ANOVA WERE CALCULATED FOR PRESENTATION. THE 6 SPECIES GROUPS INDENTED BENEATH "Burrowing Polychaetes" ARE INCLUDED WITHIN THAT GROUP.

SPECIES OR SPECIES GROUP	GREATER DENSITY ____ PATCH
Crustacea(Arthropoda)	
Corophium sp.	inside
Cumella vulgaris	inside
Leptochelia dubia	inside
Paraphoxus sp.	inside
Polychaetes (Annelida)	
Haploscoloplos elongatus	inside
Lumbrineris zonata	inside
Burrowing Polychaetes	inside
Spionid Polychaetes	outside
Bivalvia (Mollusca)	
Gemma gemma	inside
Transennella sp. (white morph)	inside
Transennella tantilla (brown morph)	inside

TABLE 8.

SUMMARY OF ANOVA, MAIN EFFECT "C"- SAMPLE LOCATION WITH RESPECT TO INSIDE OR OUTSIDE OF *A. RUBROCINCTA* PATCH.

COROPHIUM SP.

SAMPLING TIME		STUDY SITE 1	2	3
JU '75	L	487.02	344.17	168.61
	W	100.34	617.61	568.15
	R	569.71	466.86	1523.15
SP '75	L	1337.42	1523.74	161.43
	W	217.67	1890.15	1739.38
	R	213.55	466.86	3120.07
D '75	L	618.08	425.03	248.19
	W	119.22	3447.96	972.27
	R	68.83	1677.66	2604.86
MR '76	L	457.25	510.49	0.00
	W	741.78	1079.64	650.70
	R	734.96	297.07	662.04
JU '76	L	640.20	73.01	68.83
	W	831.28	2578.46	765.36
	R	276.41	73.01	5976.60

TABLE 9.

95% CONFIDENCE INTERVALS ABOUT THE MEAN DENSITIES FOR 3 STUDY SITES AND 5 SAMPLING TIMES. L (OUTSIDE LEFT), R (OUTSIDE RIGHT), AND W (WITHIN) GIVE THE SAMPLE LOCATION WITH RESPECT TO THE A. RUBROCINCTA PATCH AT EACH STUDY SITE.

TABLE 10. COROPHIUM SP.

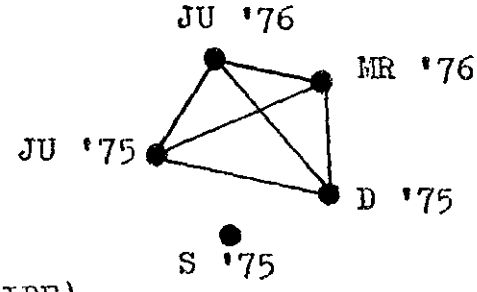
I. 3-WAY ANOVA (OUTSIDE LEFT AND WITHIN PATCHES)

A	B	C	AB	AC	BC	ABC	REPS.
*	**	***	NS	***	*	NS	**

DECOMPOSED MAIN EFFECTS

	COMPARISON	SIGNIFICANCE
A (STUDY SITES)	1 vs. 2,3	NS
	2 vs. 1,3	NS

B (SAMPLING TIMES)



C (DENSITY WITHIN > DENSITY OUTSIDE)

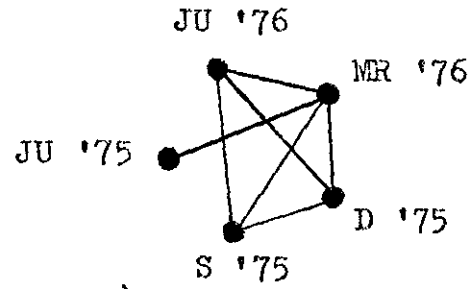
II. 3- WAY ANOVA (OUTSIDE RIGHT AND WITHIN PATCHES)

A	B	C	AB	AC	BC	ABC	REPS.
***	**	*	**	***	NS	NS	***

DECOMPOSED MAIN EFFECTS

	COMPARISON	SIGNIFICANCE
A (STUDY SITES)	1 vs. 2,3	**
	2 vs. 1,3	NS

B (SAMPLING TIMES)



C (DENSITY WITHIN > DENSITY OUTSIDE)

CUMELLA VULGARIS

SAMPLING TIME		STUDY SITE 1	2	3
JU '75	L	0.00	0.00	0.00
	W	54.56	54.56	0.00
	R	0.00	0.00	0.00
SP '75	L	54.56	0.00	0.00
	W	384.23	0.00	109.12
	R	0.00	0.00	0.00
D '75	L	0.00	54.56	69.01
	W	885.09	161.84	411.17
	R	0.00	109.12	645.98
MR '76	L	163.67	0.00	1232.53
	W	2414.94	368.40	1811.37
	R	262.78	54.56	73.20
JU '76	L	0.00	0.00	0.00
	W	1332.78	0.00	1127.62
	R	0.00	0.00	1838.96

TABLE 11.

95% CONFIDENCE INTERVALS ABOUT THE MEAN DENSITIES FOR 3 STUDY SITES AND 5 SAMPLING TIMES. L (OUTSIDE LEFT), R (OUTSIDE RIGHT), AND W (WITHIN) GIVE THE SAMPLE LOCATION WITH RESPECT TO THE A. RUBROCINCTA PATCH AT EACH STUDY SITE.

TABLE 12. CUMELLA VULGARIS

I. 3-WAY ANOVA (OUTSIDE LEFT AND WITHIN PATCHES)

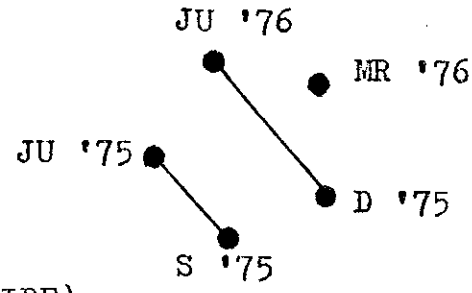
A	B	C	AB	AC	BC	ABC	REPS.
***	***	***	*	***	***	*	***

DECOMPOSED MAIN EFFECTS

A (STUDY SITES)

COMPARISON	SIGNIFICANCE
1 vs. 2,3	*
2 vs. 1,3	**

B (SAMPLING TIMES)



C (DENSITY WITHIN > DENSITY OUTSIDE)

II. 3- WAY ANOVA (OUTSIDE RIGHT AND WITHIN PATCHES)

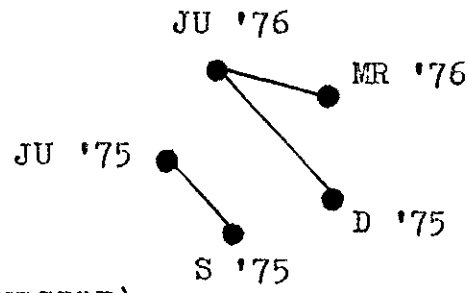
A	B	C	AB	AC	BC	ABC	REPS.
***	***	***	***	***	***	NS	***

DECOMPOSED MAIN EFFECTS

A (STUDY SITES)

COMPARISON	SIGNIFICANCE
1 vs. 2,3	*
2 vs. 1,3	**

B (SAMPLING TIMES)



C (DENSITY WITHIN > DENSITY OUTSIDE)

LEPTOCHELIA DUBIA

SAMPLING TIME		STUDY SITE 1	2	3
JU '75	L	2152.17	0.00	0.00
	W	797.20	54.42	801.64
	R	1915.06	0.00	0.00
SP '75	L	4236.67	68.83	54.42
	W	1368.29	68.83	656.65
	R	3736.82	0.00	54.42
D '75	L	23668.44	54.42	163.25
	W	4249.44	68.83	557.10
	R	3930.55	108.84	131.06
MR '76	L	16365.92	1115.26	100.35
	W	12188.14	671.37	557.10
	R	29509.28	100.34	54.42
JU '76	L	12798.50	54.42	54.42
	W	2711.80	177.17	6283.14
	R	2242.84	163.25	2764.69

TABLE 13.

95% CONFIDENCE INTERVALS ABOUT THE MEAN DENSITIES FOR 3 STUDY SITES AND 5 SAMPLING TIMES. L (OUTSIDE LEFT), R (OUTSIDE RIGHT), AND W (WITHIN) GIVE THE SAMPLE LOCATION WITH RESPECT TO THE A. RUBROCINCTA PATCH AT EACH STUDY SITE.

TABLE 14. LEPTOCHELIA DUBIA

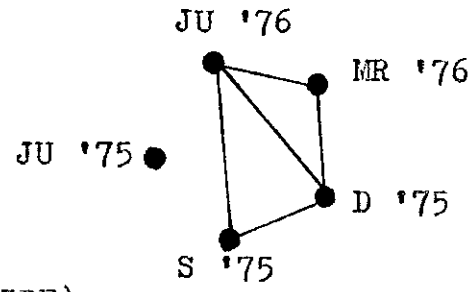
I. 3-WAY ANOVA (OUTSIDE LEFT AND WITHIN PATCHES)

A	B	C	AB	AC	BC	ABC	REPS.
***	***	**	*	***	*	NS	***

DECOMPOSED MAIN EFFECTS

	COMPARISON	SIGNIFICANCE
A (STUDY SITES)		
	1 vs. 2,3	***
	2 vs. 1,3	***

B (SAMPLING TIMES)



C (DENSITY WITHIN > DENSITY OUTSIDE)

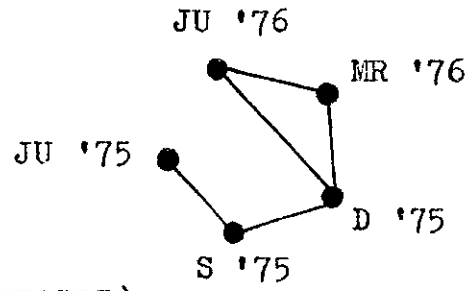
II. 3- WAY ANOVA (OUTSIDE RIGHT AND WITHIN PATCHES)

A	B	C	AB	AC	BC	ABC	REPS.
***	***	**	**	**	NS	NS	***

DECOMPOSED MAIN EFFECTS

	COMPARISON	SIGNIFICANCE
A (STUDY SITES)		
	1 vs. 2,3	***
	2 vs. 1,3	***

B (SAMPLING TIMES)



C (DENSITY WITHIN > DENSITY OUTSIDE)

PARAPHOXUS SP.

SAMPLING TIME			STUDY SITE 1	2	3
		L	1241.20	320.90	161.44
	JU '75	W	352.72	400.16	1253.41
		R	161.84	54.55	0.00
		L	214.07	267.23	69.00
	SP '75	W	356.08	530.54	730.62
		R	235.25	0.00	54.55
		L	177.59	218.19	168.61
	D '75	W	408.92	453.10	182.55
		R	161.82	218.19	0.00
		L	0.00	532.79	0.00
	MR '76	W	428.12	775.99	111.79
		R	109.10	0.00	111.79
		L	0.00	464.96	109.10
	JU '76	W	481.85	778.23	482.98
		R	54.55	0.00	54.55

TABLE 15.

95% CONFIDENCE INTERVALS ABOUT THE MEAN DENSITIES FOR 3 STUDY SITES AND 5 SAMPLING TIMES. L (OUTSIDE LEFT), R (OUTSIDE RIGHT), AND W (WITHIN) GIVE THE SAMPLE LOCATION WITH RESPECT TO THE A. RUBROCINCTA PATCH AT EACH STUDY SITE.

TABLE 16. PARAPHOXUS SP.

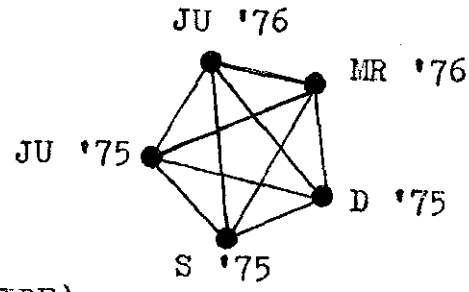
I. 3-WAY ANOVA (OUTSIDE LEFT AND WITHIN PATCHES)

A	B	C	AB	AC	BC	ABC	REPS.
***	NS	***	***	NS	NS	NS	***

DECOMPOSED MAIN EFFECTS

	COMPARISON	SIGNIFICANCE
A (STUDY SITES)		
	1 vs. 2,3	NS
	2 vs. 1,3	*

B (SAMPLING TIMES)



C (DENSITY WITHIN > DENSITY OUTSIDE)

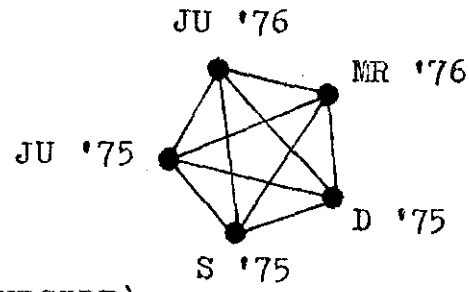
II. 3- WAY ANOVA (OUTSIDE RIGHT AND WITHIN PATCHES)

A	B	C	AB	AC	BC	ABC	REPS.
*	NS	***	*	**	NS	*	*

DECOMPOSED MAIN EFFECTS

	COMPARISON	SIGNIFICANCE
A (STUDY SITES)		
	1 vs. 2,3	NS
	2 vs. 1,3	NS

B (SAMPLING TIMES)



C (DENSITY WITHIN > DENSITY OUTSIDE)

HAPLOSCOLOPLOS ELONGATUS

SAMPLING TIME		STUDY SITE 1	2	3
JU '75	L	425.03	108.83	308.09
	W	155.83	496.36	925.13
	R	365.05	163.25	266.60
SP '75	L	515.68	427.11	168.61
	W	453.67	284.85	1023.60
	R	100.34	163.25	196.21
D '75	L	161.43	68.83	333.69
	W	196.21	429.81	196.21
	R	0.00	206.51	481.85
MR '76	L	115.30	108.84	188.51
	W	320.11	219.03	395.43
	R	54.42	0.00	0.00
JU '76	L	196.21	233.43	68.94
	W	383.26	249.38	233.43
	R	0.00	0.00	54.42

TABLE 17.

95% CONFIDENCE INTERVALS ABOUT THE MEAN DENSITIES FOR 3 STUDY SITES AND 5 SAMPLING TIMES. L (OUTSIDE LEFT), R (OUTSIDE RIGHT), AND W (WITHIN) GIVE THE SAMPLE LOCATION WITH RESPECT TO THE A. RUBROCINCTA PATCH AT EACH STUDY SITE.

TABLE 18. HAPLOSCOLOPLOS ELONGATUS

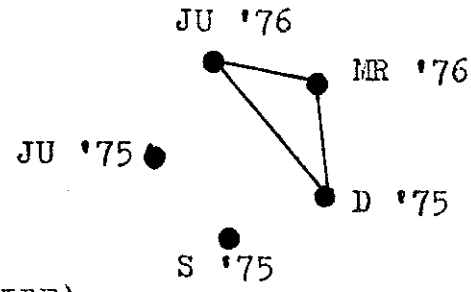
I. 3-WAY ANOVA (OUTSIDE LEFT AND WITHIN PATCHES)

A	B	C	AB	AC	BC	ABC	REPS.
***	***	***	NS	*	NS	NS	**

DECOMPOSED MAIN EFFECTS

	COMPARISON	SIGNIFICANCE
A (STUDY SITES)	1 vs. 2,3	*
	2 vs. 1,3	NS

B (SAMPLING TIMES)



C (DENSITY WITHIN > DENSITY OUTSIDE)

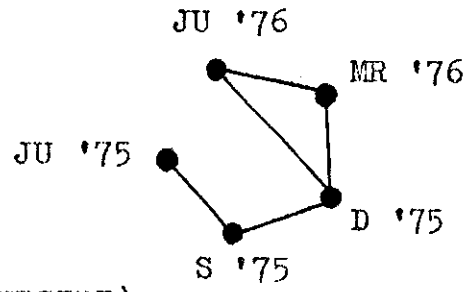
II. 3- WAY ANOVA (OUTSIDE RIGHT AND WITHIN PATCHES)

A	B	C	AB	AC	BC	ABC	REPS.
***	***	***	NS	**	NS	NS	**

DECOMPOSED MAIN EFFECTS

	COMPARISON	SIGNIFICANCE
A (STUDY SITES)	1 vs. 2,3	*
	2 vs. 1,3	NS

B (SAMPLING TIMES)



C (DENSITY WITHIN > DENSITY OUTSIDE)

LUMBRINERIS ZONATA

SAMPLING TIME		STUDY SITE 1	2	3
JU '75	L	822.39	200.45	160.36
	W	119.46	213.81	581.30
	R	261.93	111.85	130.96
SP '75	L	1091.13	374.18	240.60
	W	119.46	395.56	815.17
	R	100.63	155.02	2071.34
D '75	L	681.54	155.02	240.54
	W	163.71	160.36	100.23
	R	109.18	320.73	280.63
MR '76	L	196.72	112.25	137.64
	W	163.71	360.81	551.91
	R	68.89	111.86	161.70
JU '76	L	111.86	72.16	160.36
	W	207.14	200.45	367.50
	R	109.18	54.53	54.53

TABLE 19.

95% CONFIDENCE INTERVALS ABOUT THE MEAN DENSITIES FOR 3 STUDY SITES AND 5 SAMPLING TIMES. L (OUTSIDE LEFT), R (OUTSIDE RIGHT), AND W (WITHIN) GIVE THE SAMPLE LOCATION WITH RESPECT TO THE A. RUBROCINCTA PATCH AT EACH STUDY SITE.

TABLE 20. LUMBRINERIS ZONATA

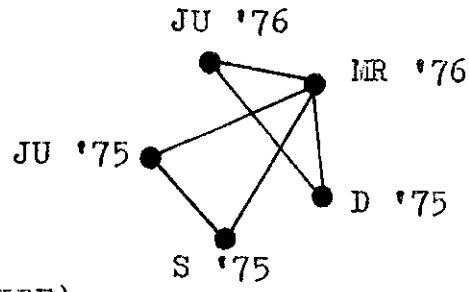
I. 3-WAY ANOVA (OUTSIDE LEFT AND WITHIN PATCHES)

A	B	C	AB	AC	BC	ABC	REPS.
***	***	NS	NS	***	NS	NS	***

DECOMPOSED MAIN EFFECTS

	COMPARISON	SIGNIFICANCE
A (STUDY SITES)	1 vs. 2,3	*
	2 vs. 1,3	NS

B (SAMPLING TIMES)



C (DENSITY WITHIN DENSITY OUTSIDE)

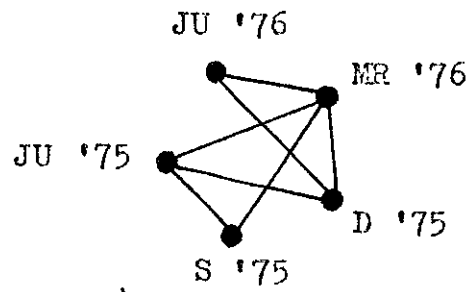
II. 3- WAY ANOVA (OUTSIDE RIGHT AND WITHIN PATCHES)

A	B	C	AB	AC	BC	ABC	REPS.
***	***	***	NS	**	*	*	NS

DECOMPOSED MAIN EFFECTS

	COMPARISON	SIGNIFICANCE
A (STUDY SITES)	1 vs. 2,3	**
	2 vs. 1,3	NS

B (SAMPLING TIMES)



C (DENSITY WITHIN > DENSITY OUTSIDE)

BURROWING POLYCHAETES

SAMPLING TIME		STUDY SITE 1	2	3
JU '75	L	1214.17	161.43	380.93
	W	233.43	623.81	1339.43
	R	530.97	200.68	331.02
SP '75	L	1313.52	776.12	377.21
	W	679.69	410.13	1232.32
	R	386.33	373.87	1978.35
D '75	L	993.95	438.06	807.15
	W	594.13	600.10	182.13
	R	949.89	542.56	984.67
MR '76	L	308.80	427.81	308.80
	W	602.06	627.59	1336.76
	R	671.37	586.62	489.16
JU '76	L	435.35	248.19	100.34
	W	672.78	287.96	263.24
	R	594.64	380.93	219.03

TABLE 21.

95% CONFIDENCE INTERVALS ABOUT THE MEAN DENSITIES FOR 3 STUDY SITES AND 5 SAMPLING TIMES. L (OUTSIDE LEFT), R (OUTSIDE RIGHT), AND W (WITHIN) GIVE THE SAMPLE LOCATION WITH RESPECT TO THE A. RUBROCINCTA PATCH AT EACH STUDY SITE.

TABLE 22. BURROWING POLYCHAETES

I. 3-WAY ANOVA (OUTSIDE LEFT AND WITHIN PATCHES)

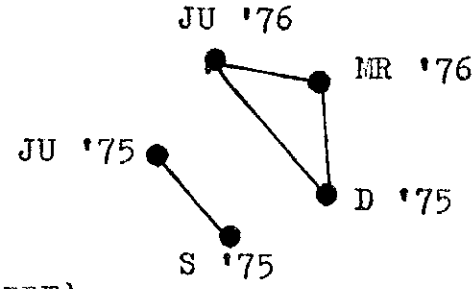
A	B	C	AB	AC	BC	ABC	REPS.
***	***	*	NS	**	NS	NS	**

DECOMPOSED MAIN EFFECTS

A (STUDY SITES)

COMPARISON	SIGNIFICANCE
1 vs. 2,3	NS
2 vs. 1,3	NS

B (SAMPLING TIMES)



C (DENSITY WITHIN > DENSITY OUTSIDE)

II. 3- WAY ANOVA (OUTSIDE RIGHT AND WITHIN PATCHES)

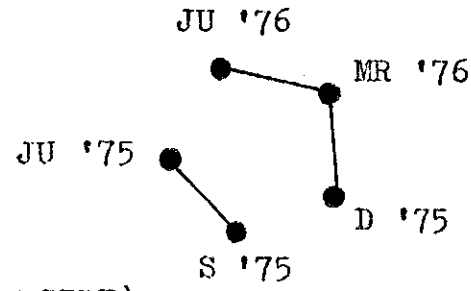
A	B	C	AB	AC	BC	ABC	REPS.
***	***	***	NS	NS	*	*	***

DECOMPOSED MAIN EFFECTS

A (STUDY SITES)

COMPARISON	SIGNIFICANCE
1 vs. 2,3	NS
2 vs. 1,3	*

B (SAMPLING TIMES)



C (DENSITY WITHIN > DENSITY OUTSIDE)

STUDY SITE	95% C.I.	SAMPLE LOCATION	SAMPLING TIME				
			1	2	3	4	5
1	UPPER	L	14.99	2116.35	139.73	139.73	22.04
		W	14.99	139.73	336.92	155.36	185.14
		R	736.94	655.84	14.99	101.85	0.00
	LOWER	L	0.34	2.76	0.18	0.18	0.29
		W	0.34	0.18	2.76	0.37	0.87
		R	0.83	2.42	0.34	0.40	0.00
2	UPPER	L	31.11	352.57	139.73	14.99	397.35
		W	0.00	0.00	0.00	0.00	74.75
		R	585.01	1345.99	377.26	667.11	2054.29
	LOWER	L	1.03	0.78	0.18	0.34	0.81
		W	0.00	0.00	0.00	0.00	0.43
		R	0.85	2.56	0.82	2.43	13.64
3	UPPER	L	234.30	74.75	74.75	0.00	0.00
		W	139.73	0.00	14.99	0.00	22.04
		R	234.30	1133.93	1153.14	185.14	1729.89
	LOWER	L	0.87	0.43	0.43	0.00	0.00
		W	0.18	0.00	0.34	0.00	0.29
		R	0.87	11.90	2.58	0.87	10.52

TABLE 23. UPPER AND LOWER CONFIDENCE INTERVALS (C.I.) ABOUT MEAN SPIONID DENSITIES (no./m^2) (FIG. 25) ESTIMATED AT THREE STUDY SITES OVER FIVE SAMPLING TIMES. DENSITIES WERE ESTIMATED TO THE OUTSIDE LEFT (L) AND RIGHT (R) AND FROM WITHIN EACH A. RUBROCINCTA PATCH. C.I.'s ARE ASYMETRIC ABOUT THE MEANS (FIG. 25) DUE TO A PREVIOUS LOG_{10} DATA TRANSFORMATION FOR ANOVA.

TABLE 24. SPIONID POLYCHAETES

I. 3-WAY ANOVA (OUTSIDE LEFT AND WITHIN PATCHES)

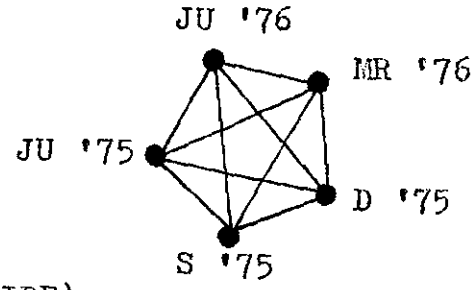
A	B	C	AB	AC	BC	ABC	REPS.
*	NS	*	NS	NS	NS	NS	*

DECOMPOSED MAIN EFFECTS

A (STUDY SITES)

COMPARISON	SIGNIFICANCE
1 vs. 2,3	*
2 vs. 1,3	NS

B (SAMPLING TIMES)



C (DENSITY WITHIN < DENSITY OUTSIDE)

II. 3- WAY ANOVA (OUTSIDE RIGHT AND WITHIN PATCHES)

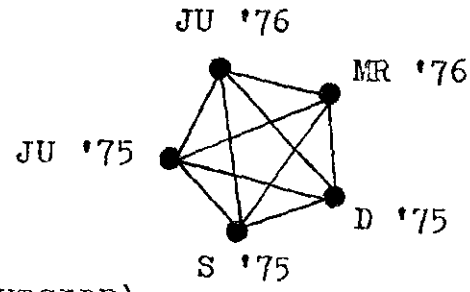
A	B	C	AB	AC	BC	ABC	REPS.
NS	NS	***	NS	***	NS	NS	**

DECOMPOSED MAIN EFFECTS

A (STUDY SITES)

COMPARISON	SIGNIFICANCE
1 vs. 2,3	NS
2 vs. 1,3	NS

B (SAMPLING TIMES)



C (DENSITY WITHIN < DENSITY OUTSIDE)

GEMMA GEMMA

SAMPLING TIME		STUDY SITE 1	2	3
JU '75	L	54.56	735.19	894.46
	W	54.56	3133.74	272.78
	R	0.00	678.35	805.15
SP '75	L	0.00	1452.68	1021.07
	W	54.56	1397.53	2228.80
	R	163.66	0.00	288.68
D '75	L	109.12	163.66	1312.10
	W	0.00	1611.77	1785.75
	R	54.56	1001.52	1580.44
MR '76	L	163.66	958.7	956.22
	W	169.04	2577.11	1234.71
	R	0.00	757.92	445.23
JU '76	L	589.61	207.02	843.77
	W	575.82	1674.27	2234.01
	R	218.22	402.39	938.94

TABLE 25.

95% CONFIDENCE INTERVALS ABOUT THE MEAN DENSITIES FOR 3 STUDY SITES AND 5 SAMPLING TIMES. L (OUTSIDE LEFT), R (OUTSIDE RIGHT), AND W (WITHIN) GIVE THE SAMPLE LOCATION WITH RESPECT TO THE A. RUBROCINCTA PATCH AT EACH STUDY SITE.

TABLE 26. GEMMA GEMMA

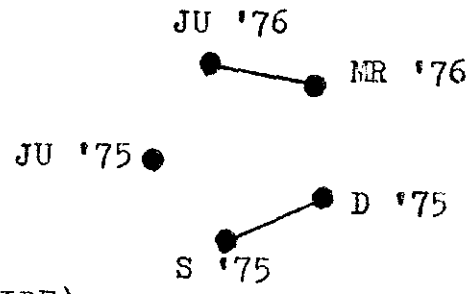
I. 3-WAY ANOVA (OUTSIDE LEFT AND WITHIN PATCHES)

A	B	C	AB	AC	BC	ABC	REPS.
***	***	***	***	***	***	**	***

DECOMPOSED MAIN EFFECTS

	COMPARISON	SIGNIFICANCE
A (STUDY SITES)	1 vs. 2,3	***
	2 vs. 1,3	**

B (SAMPLING TIMES)



C (DENSITY WITHIN > DENSITY OUTSIDE)

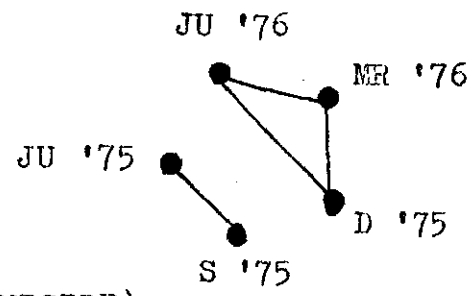
II. 3- WAY ANOVA (OUTSIDE RIGHT AND WITHIN PATCHES)

A	B	C	AB	AC	BC	ABC	REPS.
***	***	***	*	***	***	NS	*

DECOMPOSED MAIN EFFECTS

	COMPARISON	SIGNIFICANCE
A (STUDY SITES)	1 vs. 2,3	***
	2 vs. 1,3	**

B (SAMPLING TIMES)



C (DENSITY WITHIN > DENSITY OUTSIDE)

TRANSENNELLA SP. (WHITE MORPH)

SAMPLING TIME		STUDY SITE 1	2	3
JU '75	L	377.91	168.60	262.73
	W	156.20	489.17	477.13
	R	213.55	402.31	100.58
SP '75	L	73.19	496.98	916.66
	W	54.55	910.93	1191.08
	R	742.98	109.09	234.70
D '75	L	163.64	258.71	374.66
	W	155.88	828.89	441.43
	R	54.55	655.29	233.43
MR '76	L	196.21	751.09	196.21
	W	177.17	1141.93	213.55
	R	223.05	200.68	312.61
JU '76	L	206.99	383.26	131.06
	W	460.27	690.41	793.84
	R	131.84	258.70	455.95

TABLE 27.

95% CONFIDENCE INTERVALS ABOUT THE MEAN DENSITIES FOR 3 STUDY SITES AND 5 SAMPLING TIMES. L (OUTSIDE LEFT), R (OUTSIDE RIGHT), AND W (WITHIN) GIVE THE SAMPLE LOCATION WITH RESPECT TO THE A. RUBROCINCTA PATCH AT EACH STUDY SITE.

TABLE 28. TRANSENNELLA SP. (WHITE MORPH)

I. 3-WAY ANOVA (OUTSIDE LEFT AND WITHIN PATCHES)

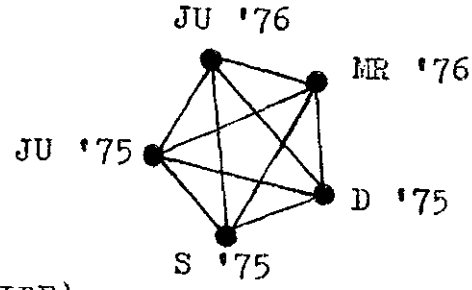
A	B	C	AB	AC	BC	ABC	REPS.
***	NS	***	*	***	***	NS	**

DECOMPOSED MAIN EFFECTS

A (STUDY SITES)

COMPARISON	SIGNIFICANCE
1 vs. 2,3	**
2 vs. 1,3	**

B (SAMPLING TIMES)



C (DENSITY WITHIN > DENSITY OUTSIDE)

II. 3- WAY ANOVA (OUTSIDE RIGHT AND WITHIN PATCHES)

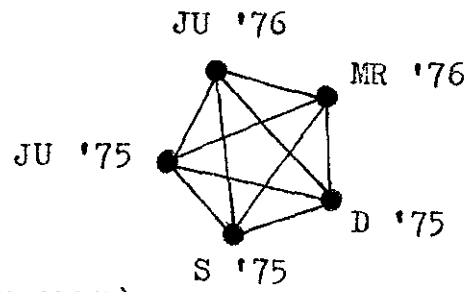
A	B	C	AB	AC	BC	ABC	REPS.
***	***	***	NS	**	NS	NS	NS

DECOMPOSED MAIN EFFECTS

A (STUDY SITES)

COMPARISON	SIGNIFICANCE
1 vs. 2,3	**
2 vs. 1,3	**

B (SAMPLING TIMES)



C (DENSITY WITHIN > DENSITY OUTSIDE)

TRANSENNELLA TANTILLA (BROWN MORPH)

SAMPLING TIME		STUDY SITE 1	2	3
JU '75	L	1303.89	177.62	736.81
	W	253.55	1329.42	2067.53
	R	545.56	138.02	478.10
SP '75	L	693.96	768.45	111.80
	W	331.85	876.98	753.10
	R	163.66	0.00	245.19
D '75	L	131.38	585.56	111.80
	W	516.99	2428.64	662.36
	R	304.73	537.32	214.09
MR '76	L	169.03	54.55	0.00
	W	396.42	537.32	688.78
	R	219.58	0.00	207.02
JU '76	L	54.55	0.00	0.00
	W	710.90	358.59	259.35
	R	0.00	54.55	0.00

TABLE 29.

95% CONFIDENCE INTERVALS ABOUT THE MEAN DENSITIES FOR 3 STUDY SITES AND 5 SAMPLING TIMES. L (OUTSIDE LEFT), R (OUTSIDE RIGHT), AND W (WITHIN) GIVE THE SAMPLE LOCATION WITH RESPECT TO THE A. RUBROCINCTA PATCH AT EACH STUDY SITE.

TABLE 30. TRANSENNELLA TANTILLA

I. 3-WAY ANOVA (OUTSIDE LEFT AND WITHIN PATCHES)

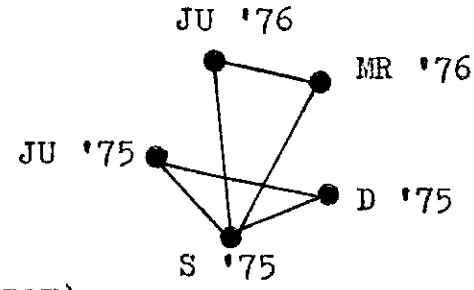
A	B	C	AB	AC	BC	ABC	REPS.
NS	***	***	*	NS	**	**	***

DECOMPOSED MAIN EFFECTS

A (STUDY SITES)

COMPARISON	SIGNIFICANCE
1 vs. 2,3	NS
2 vs. 1,3	NS

B (SAMPLING TIMES)



C (DENSITY WITHIN > DENSITY OUTSIDE)

II. 3- WAY ANOVA (OUTSIDE RIGHT AND WITHIN PATCHES)

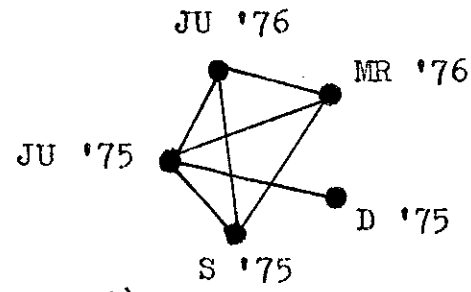
A	B	C	AB	AC	BC	ABC	REPS.
NS	*	***	*	NS	NS	NS	***

DECOMPOSED MAIN EFFECTS

A (STUDY SITES)

COMPARISON	SIGNIFICANCE
1 vs. 2,3	NS
2 vs. 1,3	NS

B (SAMPLING TIMES)



C (DENSITY WITHIN > DENSITY OUTSIDE)

SEDIMENT TYPE	SOURCE	F
OMA_1	GROUPS	$p<0.001$
	LINEAR	$p<0.001$
	QUADRATIC	$p<0.001$
OMA_2	GROUPS	$p<0.001$
	LINEAR	$p<0.001$
	QUADRATIC	$p<0.001$
MINERAL PARTICLES	GROUPS	$p<0.001$
	LINEAR	$p<0.001$
	QUADRATIC	NS

TABLE 31.

SOURCE OF PARTICLES	PARTICLE SIZE (μ)							
	1-8	9-16	17-24	25-32	33-40	41-48	49-56	>56
GUT CONTENTS	39	42	8	2	4	1	4	0
O.M.A.$_1$	37	36	12	4	3	3	3	2

TABLE 32.

TREATMENT SUBSTRATE	% OMA	RANGE OF BUILDING RATES (μ/MINUTE)
I	0 ↓ 100	37.5 - 87.5
II		300.0 - 375.0
III		375.0 - 387.5

TABLE 33.

SYMPATRIC SPIONID			AXIOTHELLA
SPECIES	ABUNDANCE		DENSITY (INDIVID./M^2)
	$TIME_0$	$TIME_{4\ WEEKS}$	
PSEUDOPOLYDORA PAUCIBRANCIATA	8	20.2±7.62	0
	8	5.6±5.45	160
	8	4.6±6.06	320
PSEUDOPOLYDORA KEMPI	0	2.8±2.39	0
	0	0.4±0.68	160
	0	0.6±1.67	320

TABLE 34.

Figure Legend

Figure — Page

Figure Page

Figure Page

Figure Page

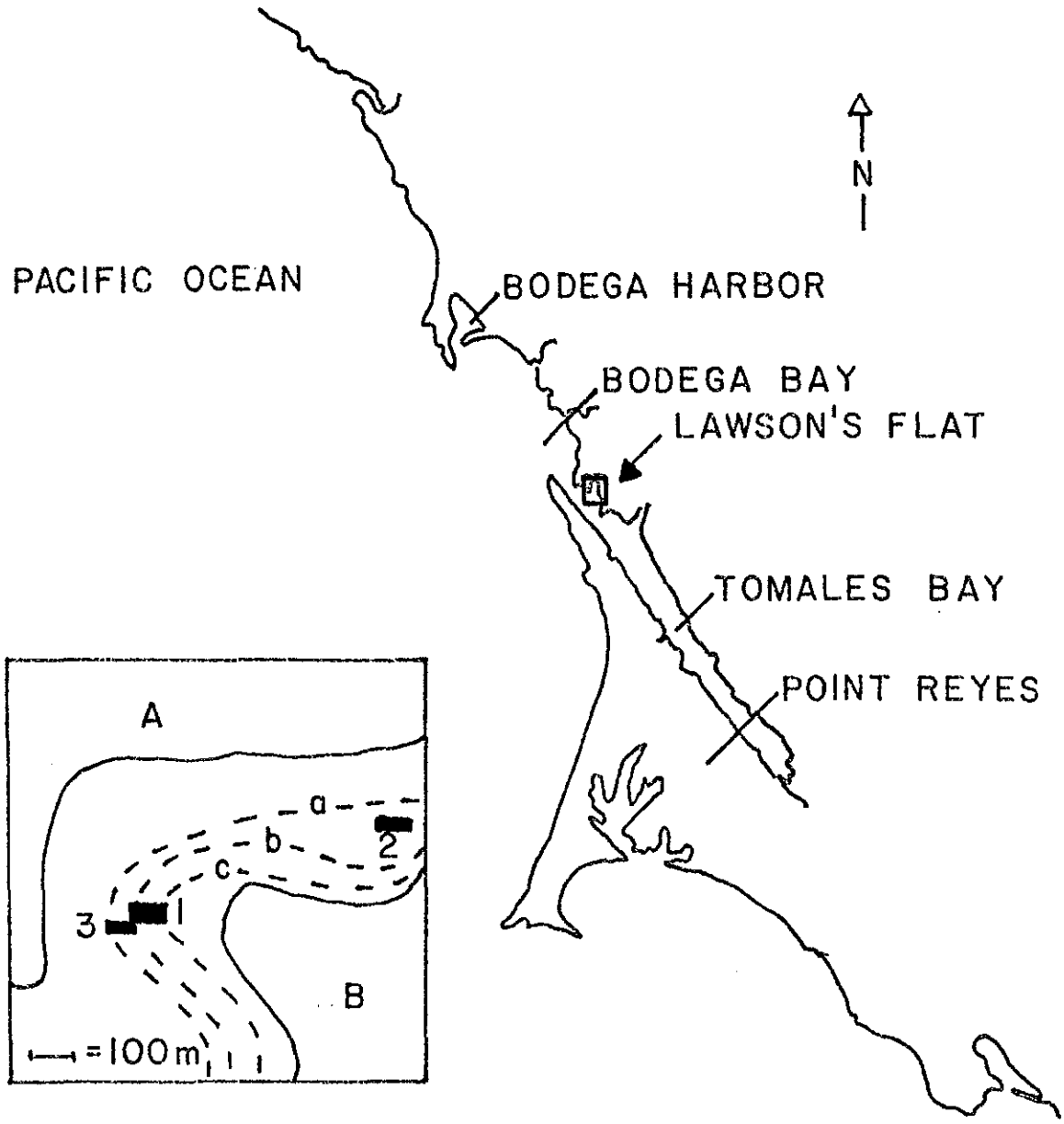

PACIFIC OCEAN
BODEGA HARBOR
BODEGA BAY
LAWSON'S FLAT
TOMALES BAY
POINT REYES
N
A
B
a
b
c
1
2
3
= 100 m

FIGURE 1

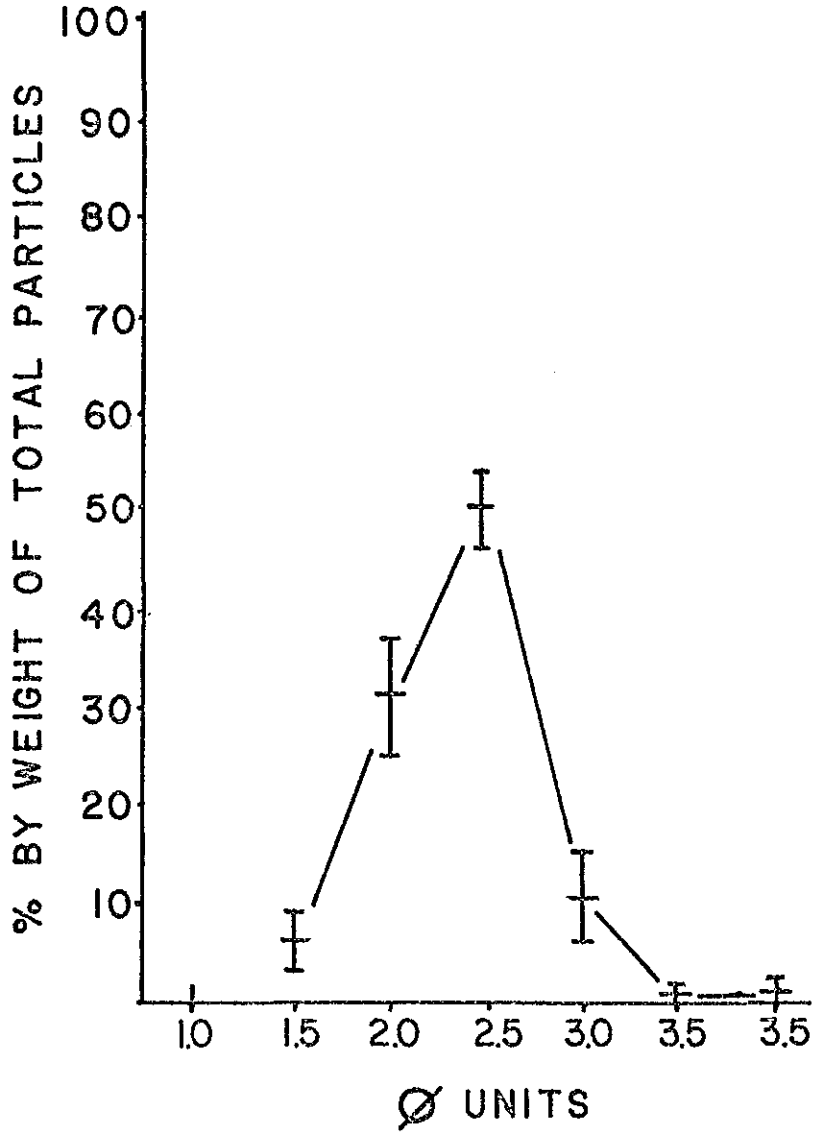

100
90
80
70
60
50
40
30
20
10
% BY WEIGHT OF TOTAL PARTICLES
1.0
1.5
2.0
2.5
3.0
3.5
3.5
Ø UNITS

FIGURE 2

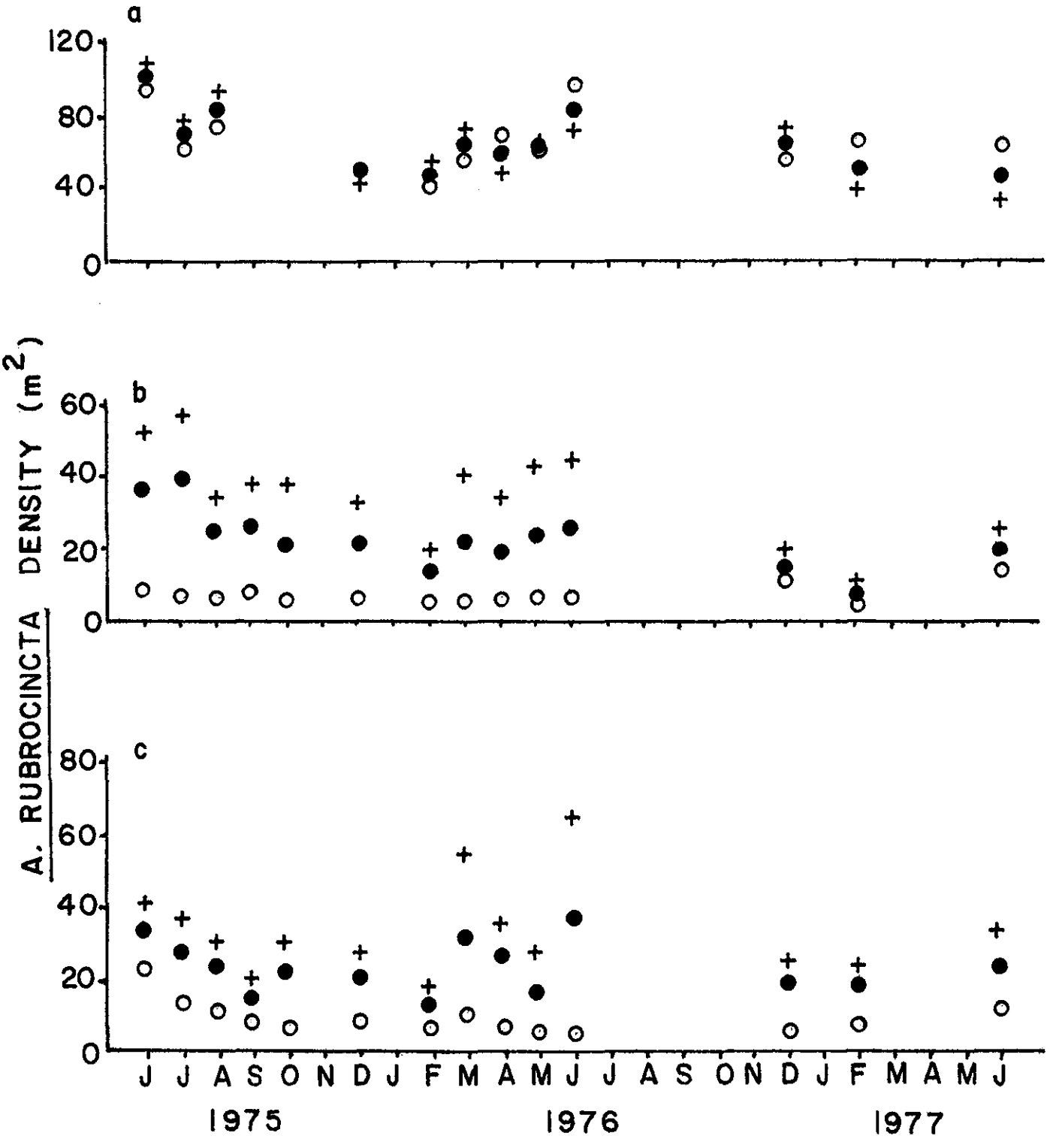

a
120
80
40
0
b
60
40
20
0
c
80
60
40
20
0
A. RUBROCINCTA DENSITY (m2)
J J A S O N D J F M A M J J A S O N D J F M A M J
1975
1976
1977
SAMPLING TIME

FIGURE 3

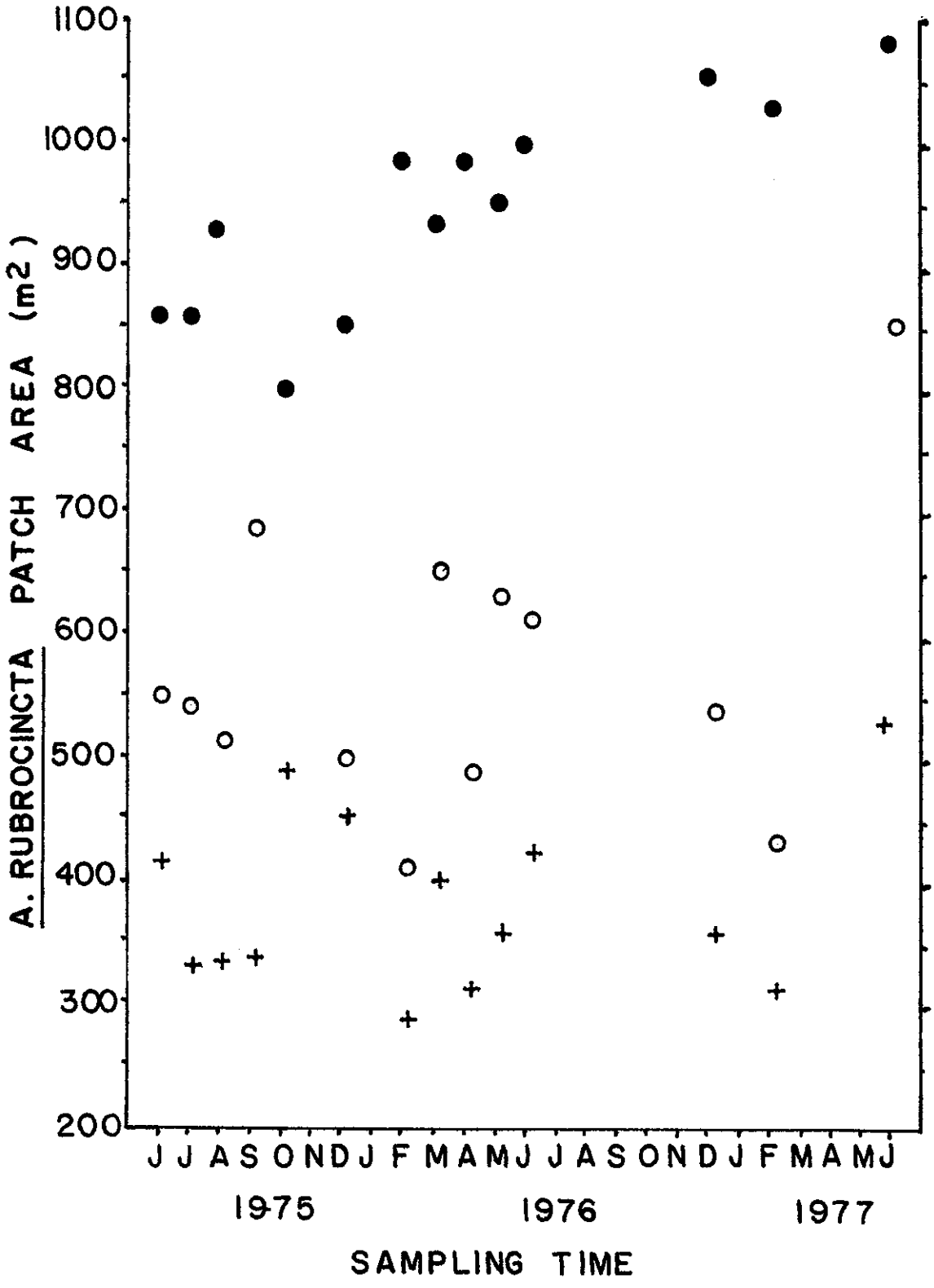
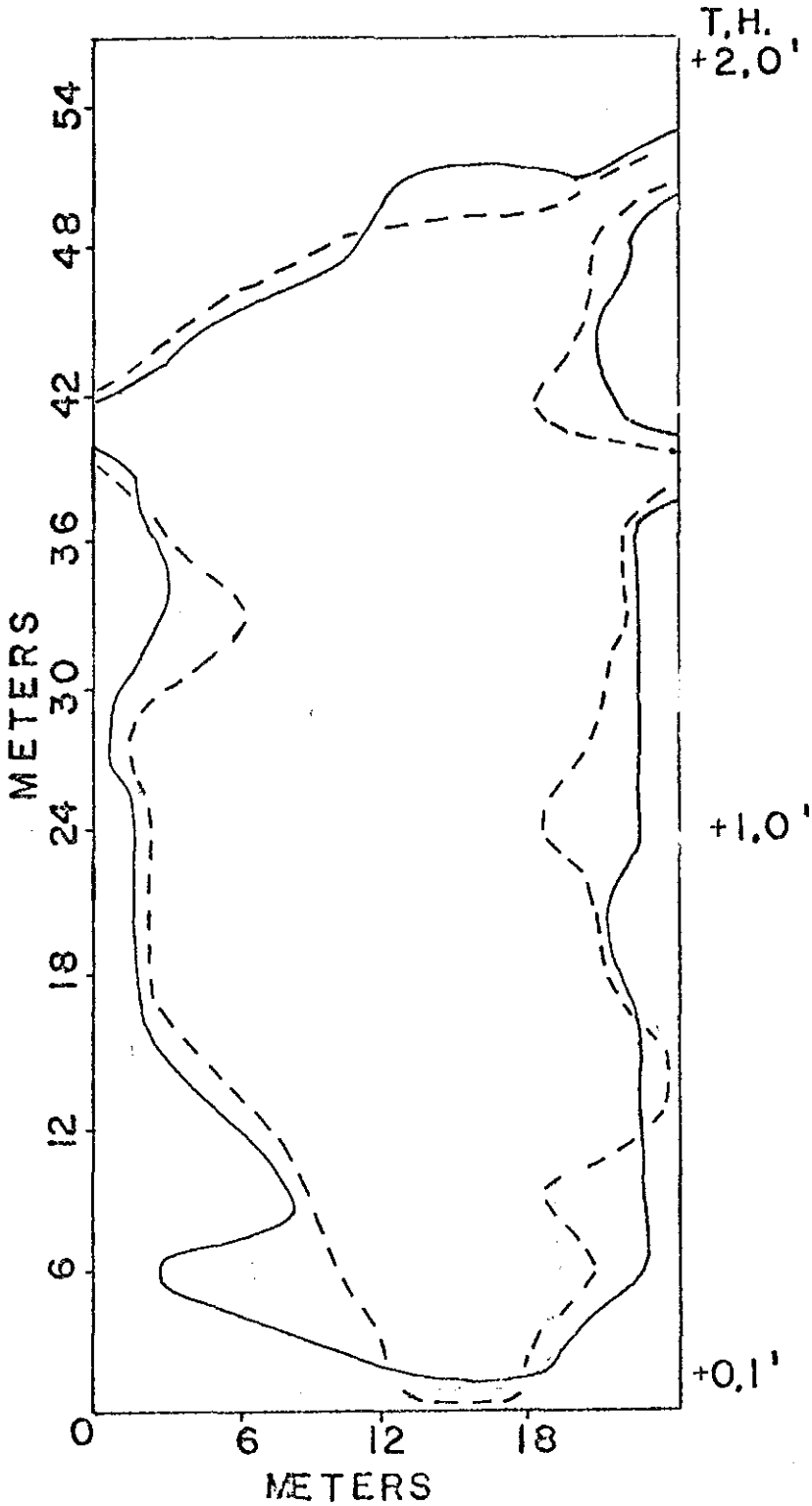
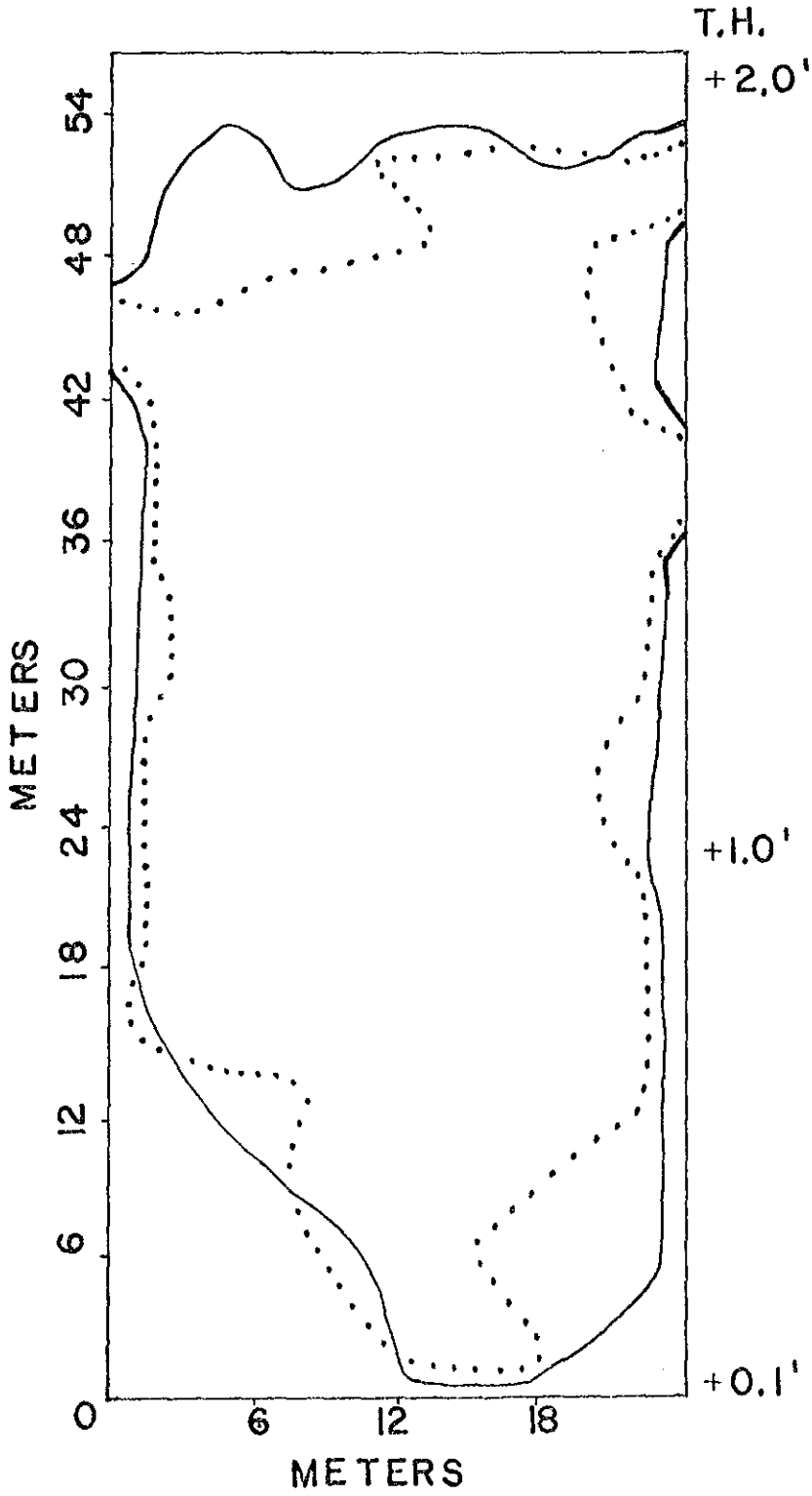

1100
1000
900
800
700
600
500
400
300
200
A. RUBROCINCTA PATCH AREA (m2)
J J A S O N D J F M A M J J A S O N D J F M A M J
1975
1976
1977
SAMPLING TIME

FIGURE 4



BED 1 — — = JUN '75
—— = FEB '76

FIGURE 5



BED I

···· = DEC '75

—— = DEC '76

FIGURE 6

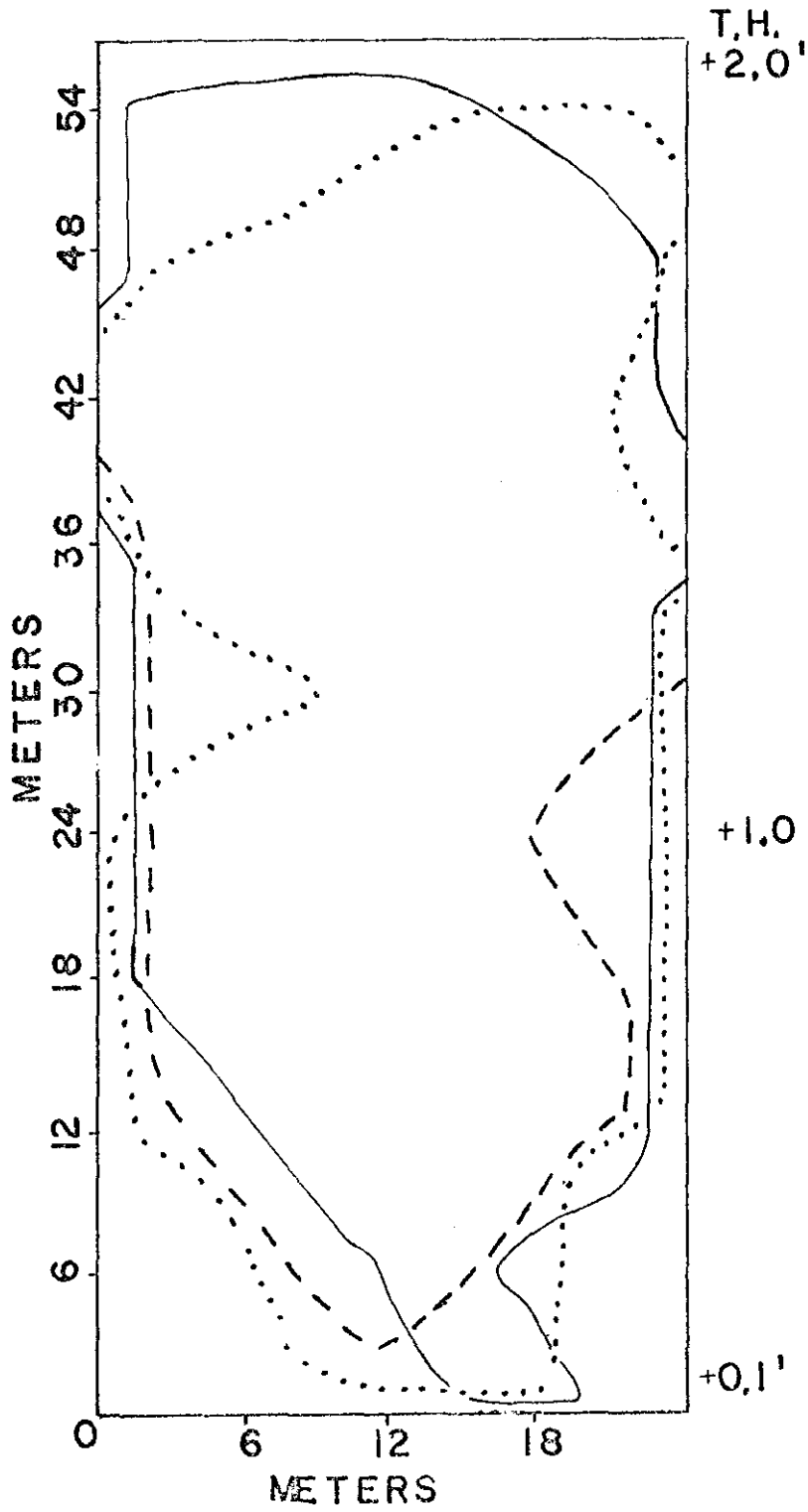

T.H.
+2.0'
+1.0'
+0.1'
METERS
0
6
12
18
24
30
36
42
48
54
0
6
12
18
METERS
BED 1 .....= JUN '76
——= FEB '77
– – –= JUN '77

FIGURE 7

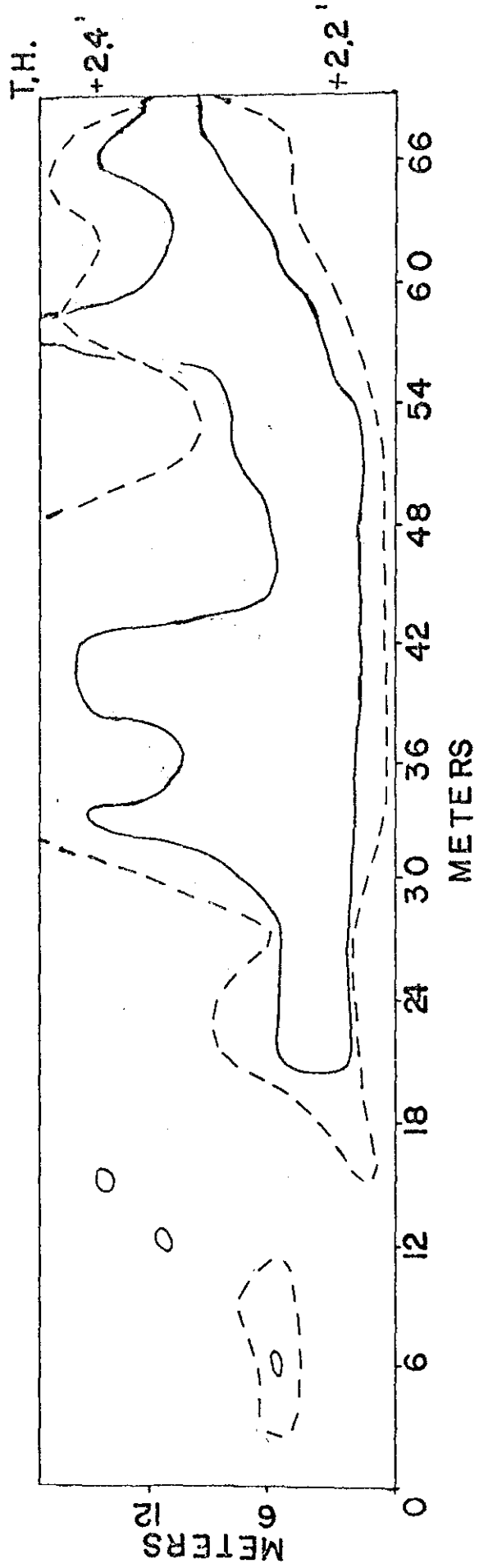

T.H.
+2.4'
+2.2'
0
6
12
METERS
0
6
12
18
24
30
36
42
48
54
60
66
METERS
BED 2
- - - = JUN '75
—— = FEB '76

FIGURE 8

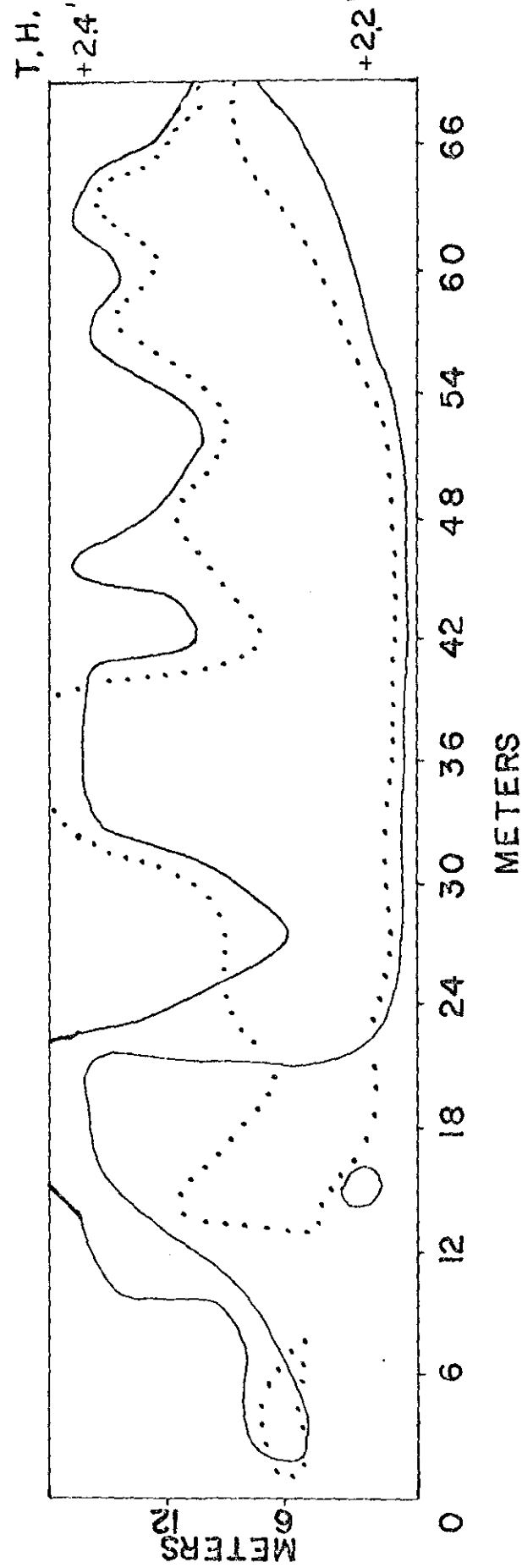
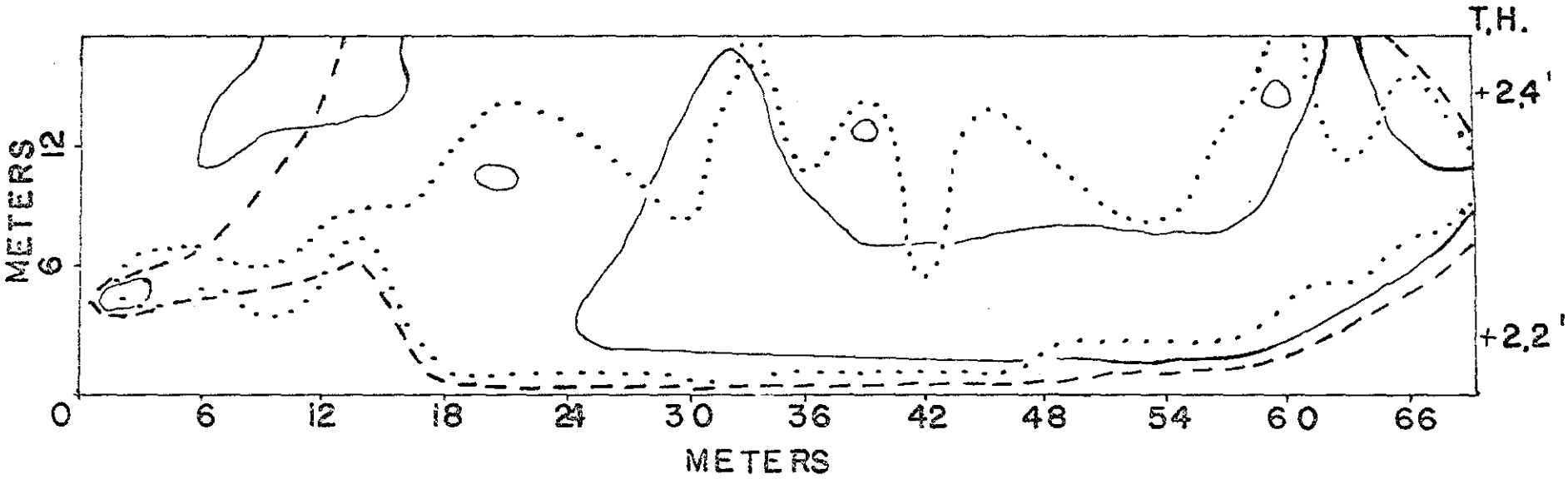

T.H.
+24'
+22'
METERS
0
6
12
18
24
30
36
42
48
54
60
66
METERS
6
12
BED 2
.... = DEC '75
—— = DEC '76

FIGURE 9



BED 2

..... = JUN '76
——— = FEB '77
- - - - = JUN '77

FIGURE 10

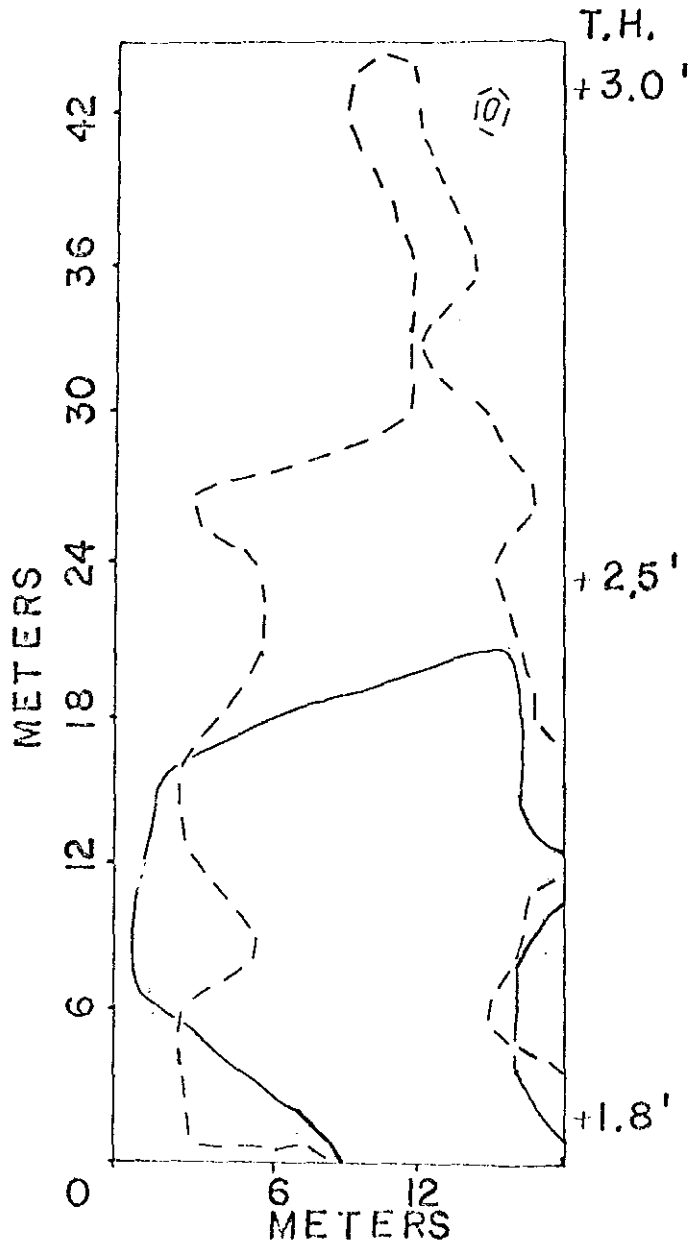

T.H.
+3.0'
+2.5'
+1.8'
(10)
METERS
0
6
12
24
30
36
42
6
12
METERS
BED 3
-- = JUN '75
—— = FEB '76

FIGURE 11

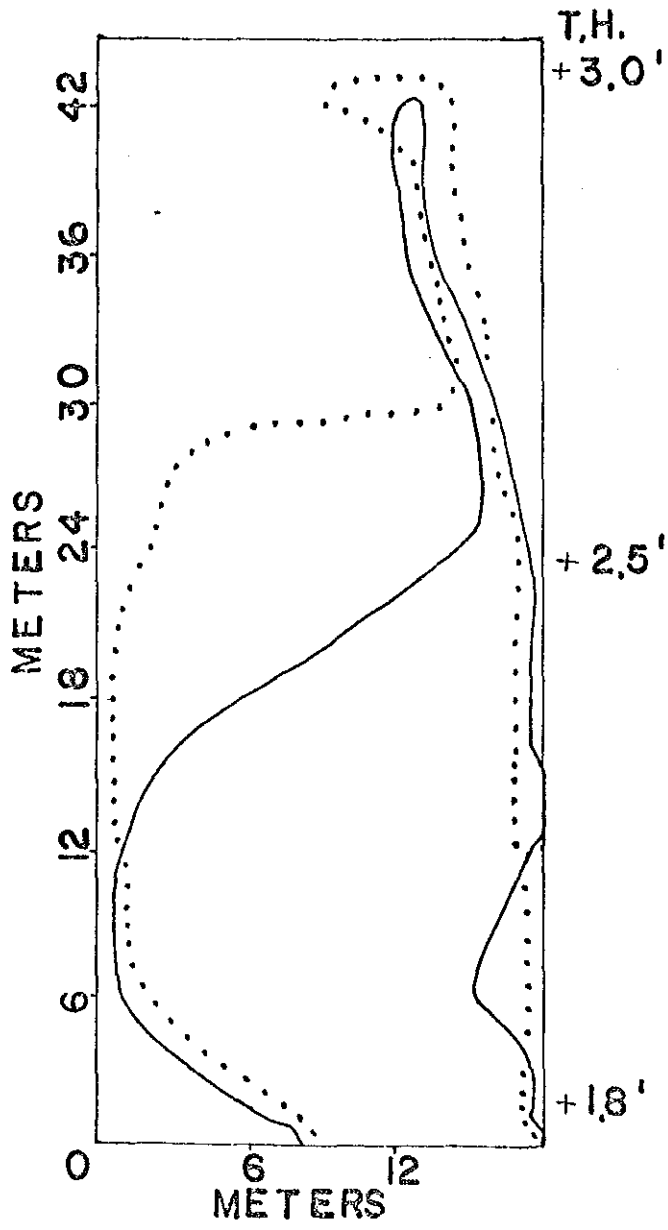
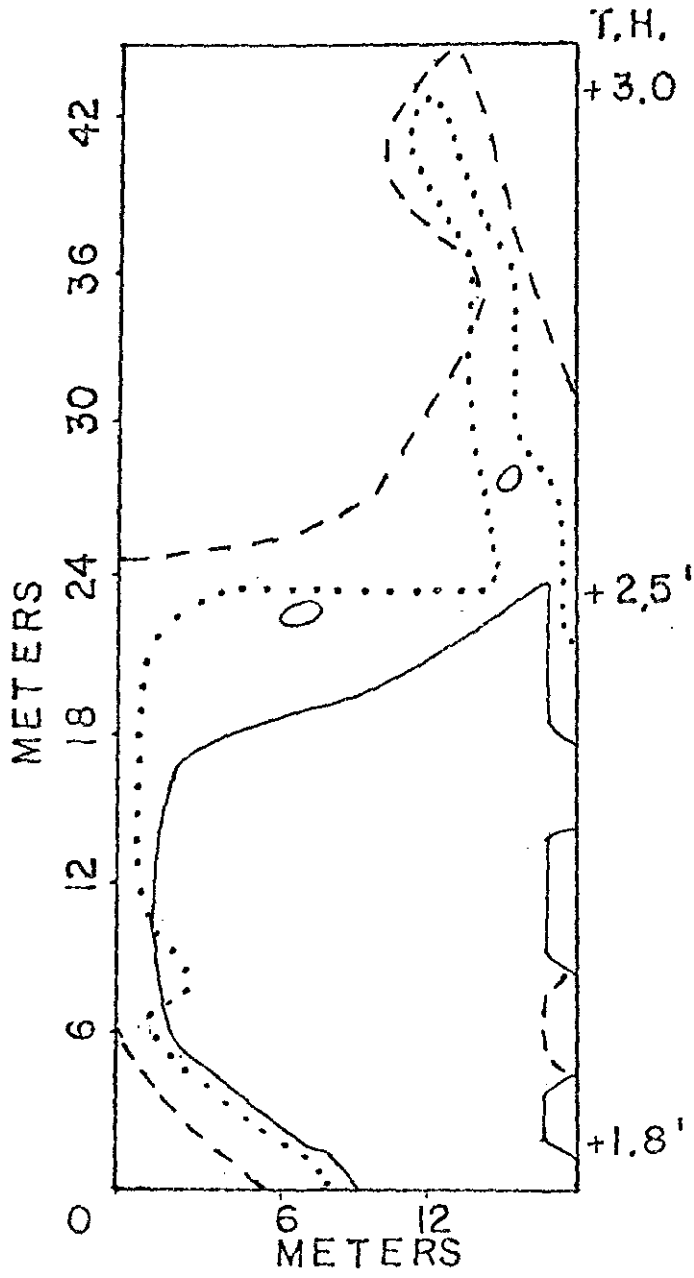


FIGURE 12



.... = JUN '76

—— = FEB '77

– – – = JUN '77

FIGURE 13

PATCH I

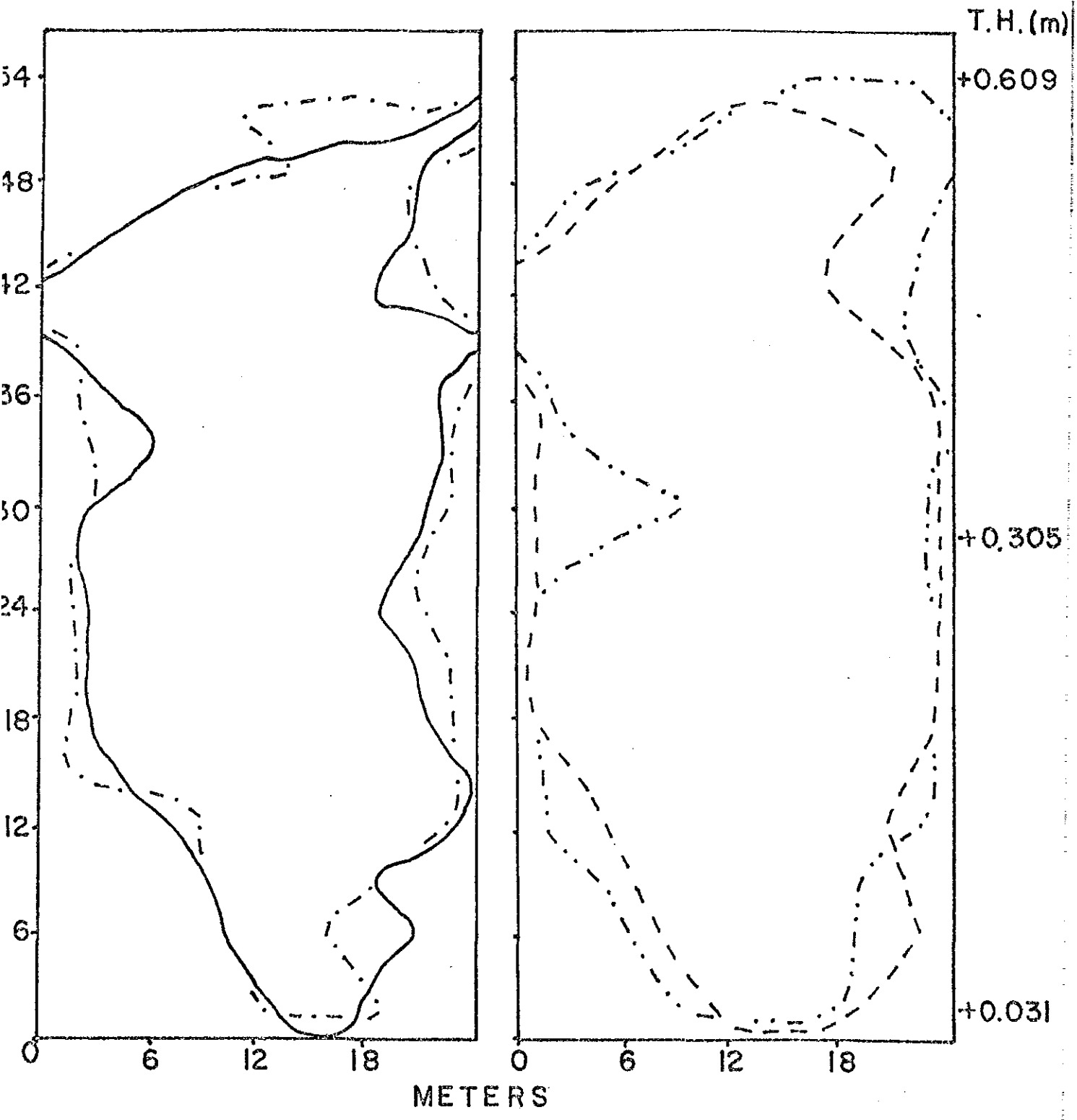


FIGURE 14

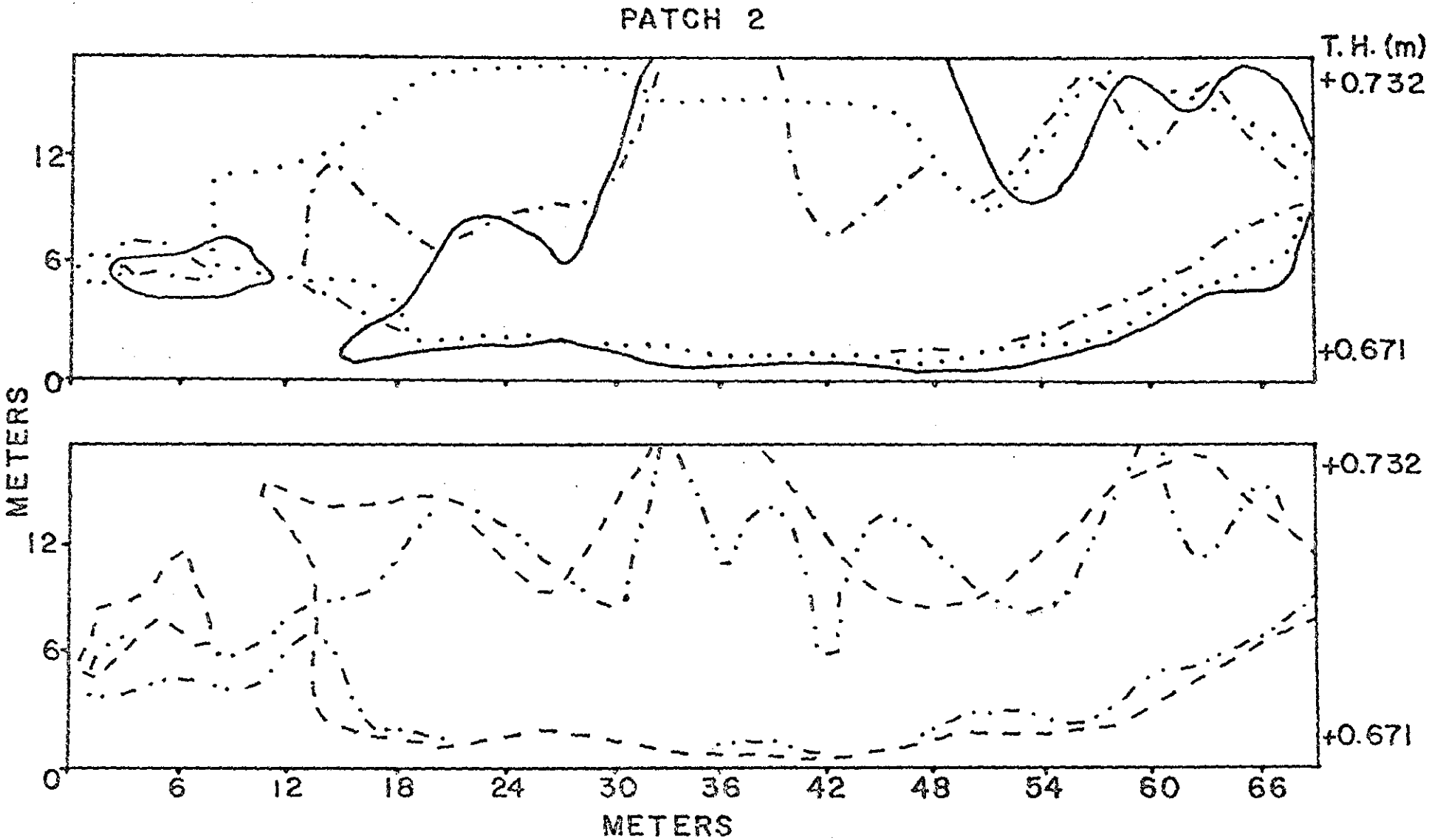

PATCH 2
T. H. (m)
+0.732
+0.671
+0.732
+0.671
12
6
0
12
6
0
METERS
6
12
18
24
30
36
42
48
54
60
66
METERS

FIGURE 15

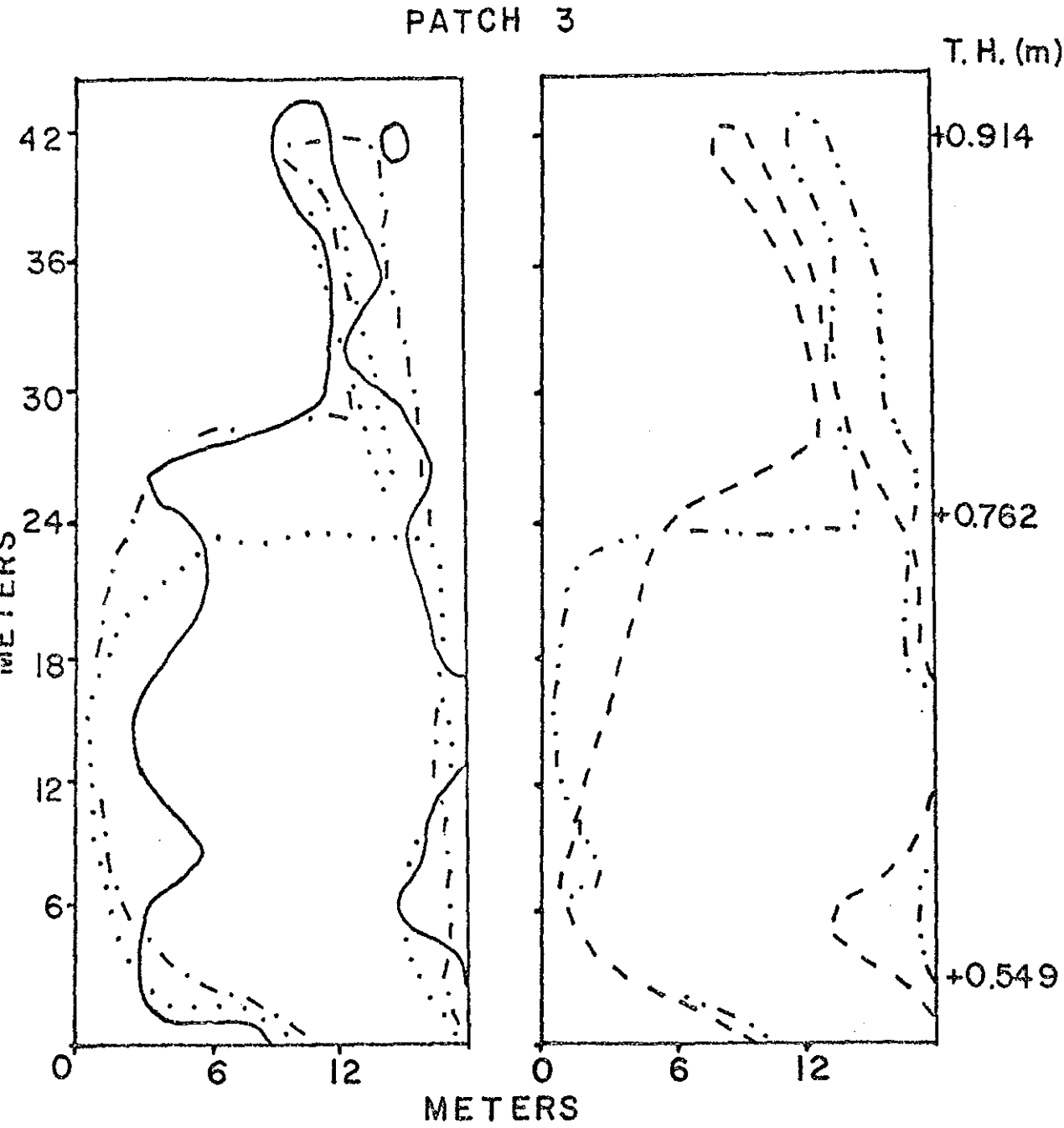

PATCH 3
T. H. (m)
+0.914
+0.762
+0.549
42
36
30
24
18
12
6
0
6
12
METERS
0
6
12
METERS

FIGURE 16

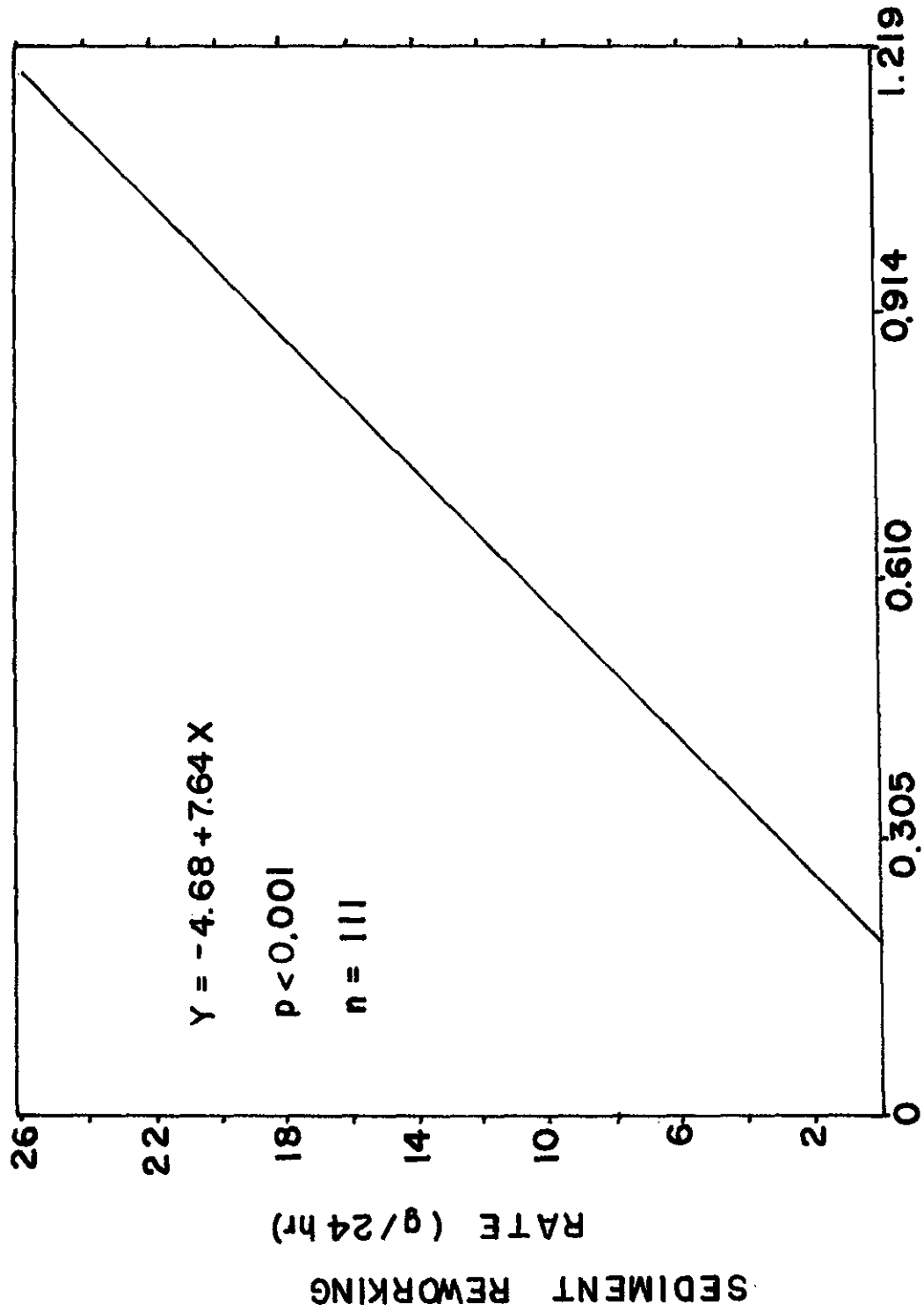

SEDIMENT REWORKING
RATE (g/24hr)
26
22
18
14
10
6
2
Y = -4.68 + 7.64 X
p<0.001
n = 111
0
0.305
0.610
0.914
1.219
TIDAL HEIGHT (m)

FIGURE 17

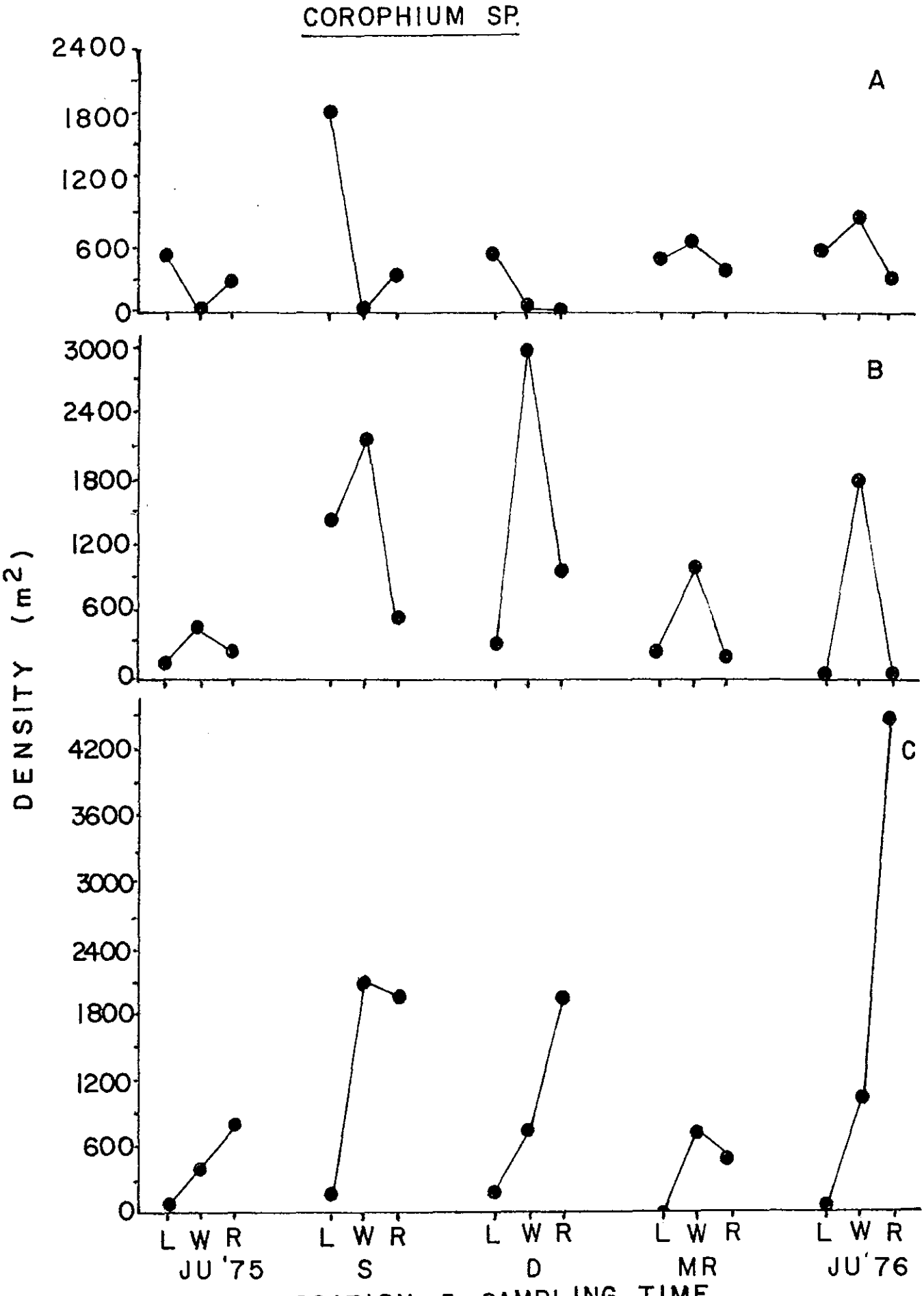

COROPHIUM SP.
A
B
C
2400
1800
1200
600
0
3000
2400
1800
1200
600
0
4200
3600
3000
2400
1800
1200
600
0
DENSITY (m²)
L W R
JU '75
L W R
S
L W R
D
L W R
MR
L W R
JU '76
LOCATION - SAMPLING TIME

FIGURE 18

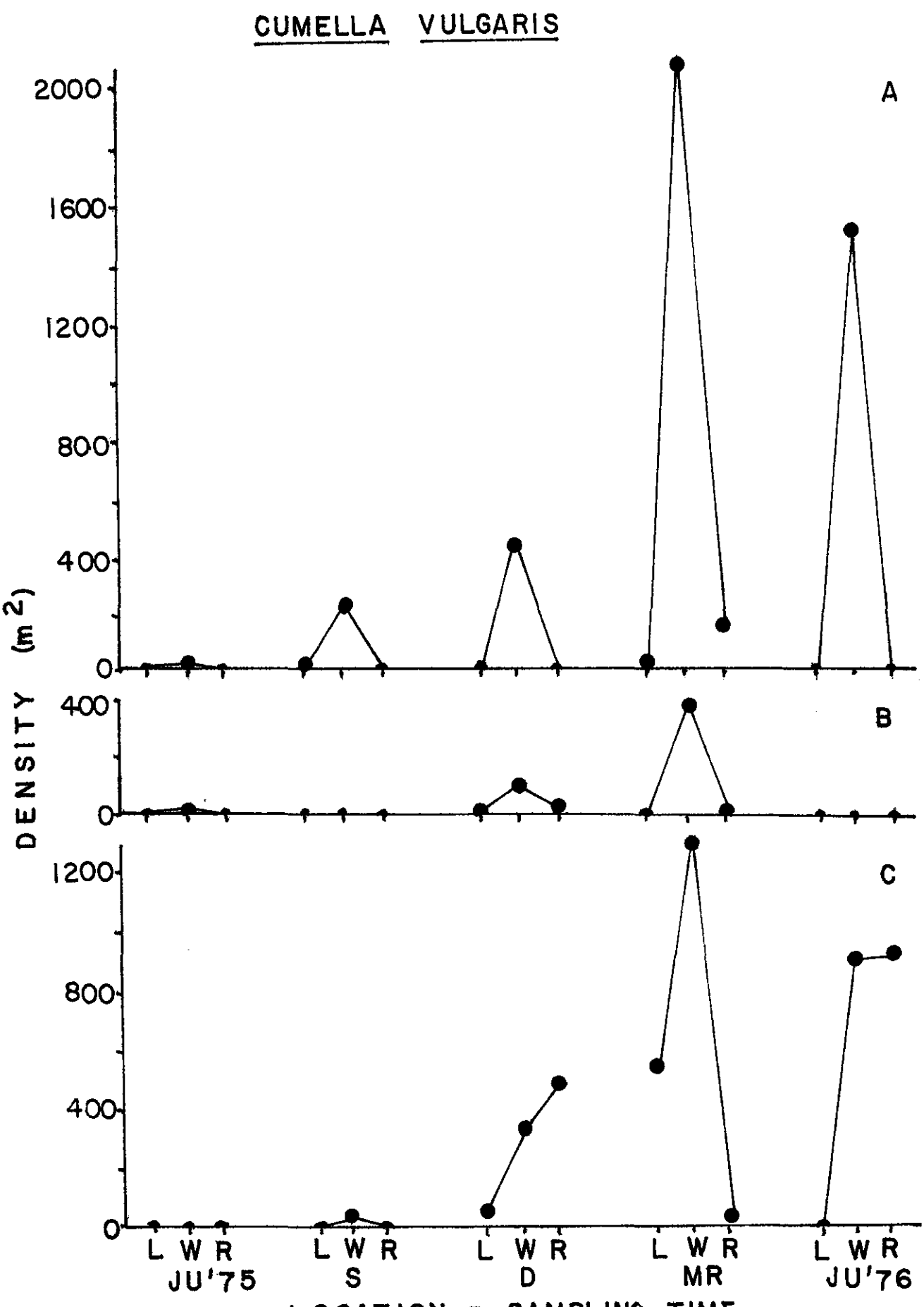

CUMELLA VULGARIS
2000
1600
1200
800
400
0
A
400
0
B
1200
800
400
0
C
DENSITY (m2)
L W R
JU'75
L W R
S
L W R
D
L W R
MR
L W R
JU'76
LOCATION - SAMPLING TIME

FIGURE 19

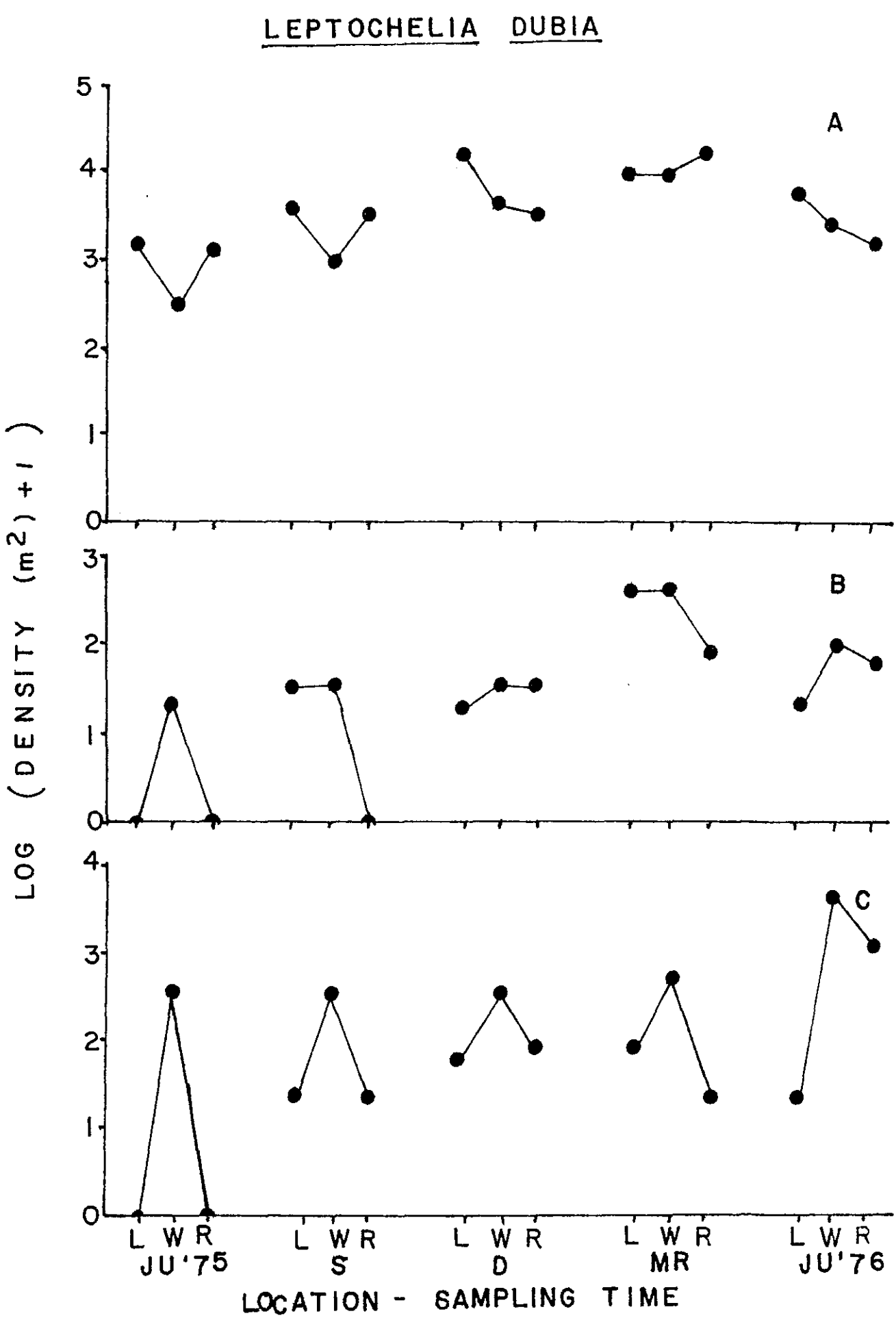

LEPTOCHELIA DUBIA
LOG (DENSITY (m2) + 1)
A
B
C
L W R
JU '75
S
D
MR
JU '76
LOCATION - SAMPLING TIME

FIGURE 20

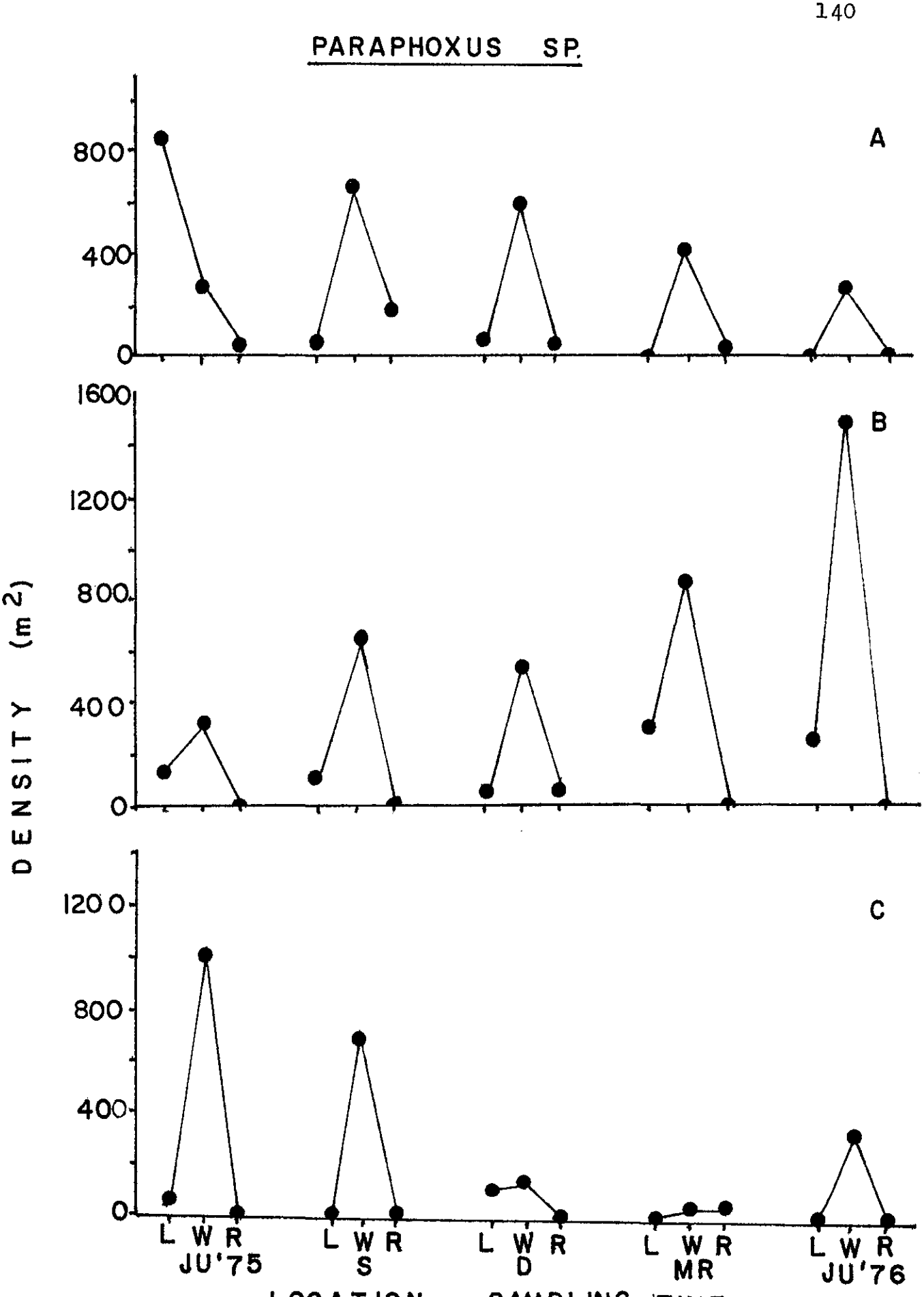

PARAPHOXUS SP.
A
800
400
0
B
1600
1200
800
400
0
C
1200
800
400
0
DENSITY (m2)
L W R
JU'75
L W R
S
L W R
D
L W R
MR
L W R
JU'76
LOCATION - SAMPLING TIME

FIGURE 21

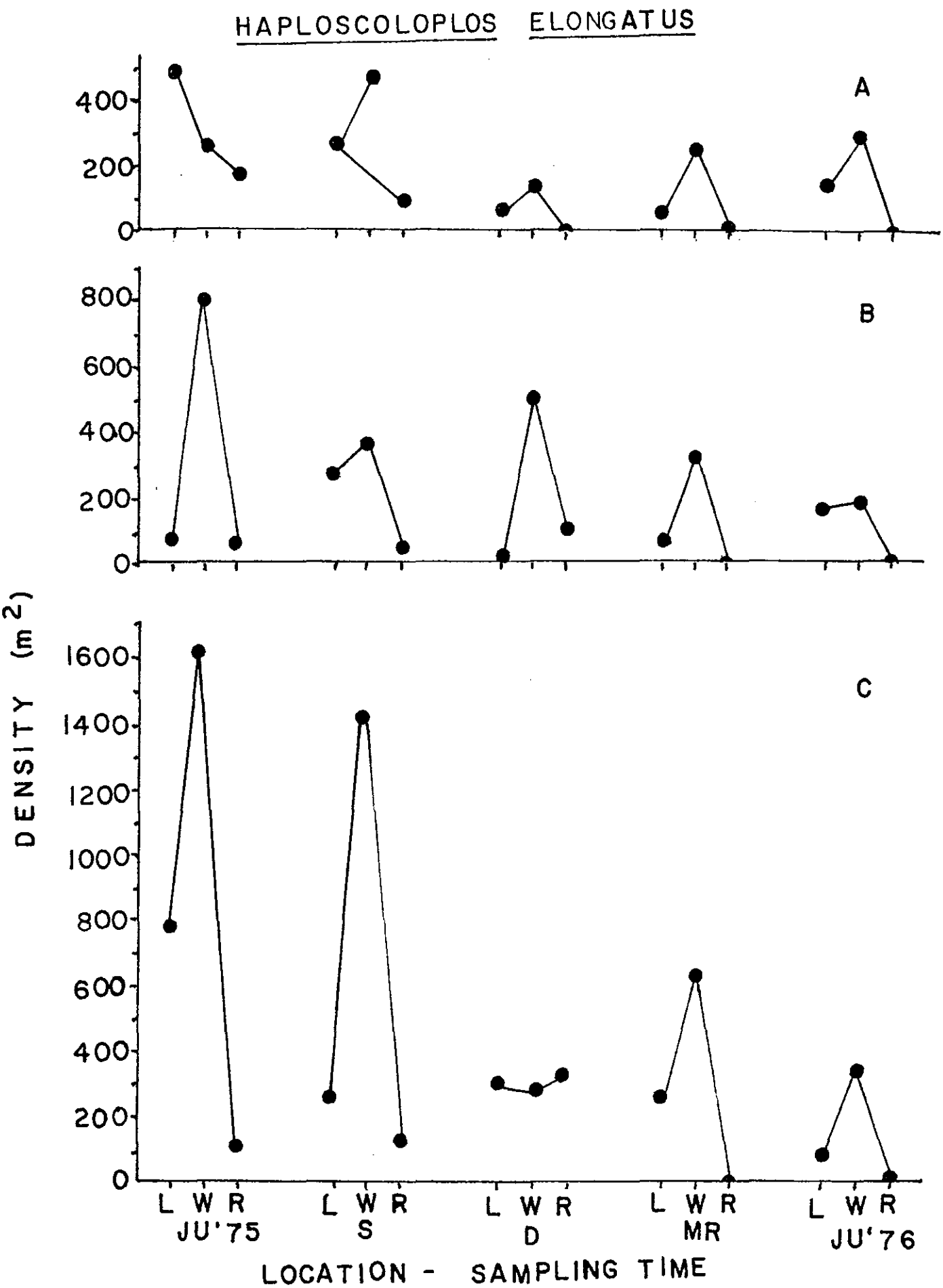

HAPLOSCOLOPLOS ELONGATUS
A
B
C
400
200
0
800
600
400
200
0
1600
1400
1200
1000
800
600
400
200
0
DENSITY (m2)
L W R
JU'75
L W R
S
L W R
D
L W R
MR
L W R
JU'76
LOCATION - SAMPLING TIME

FIGURE 22

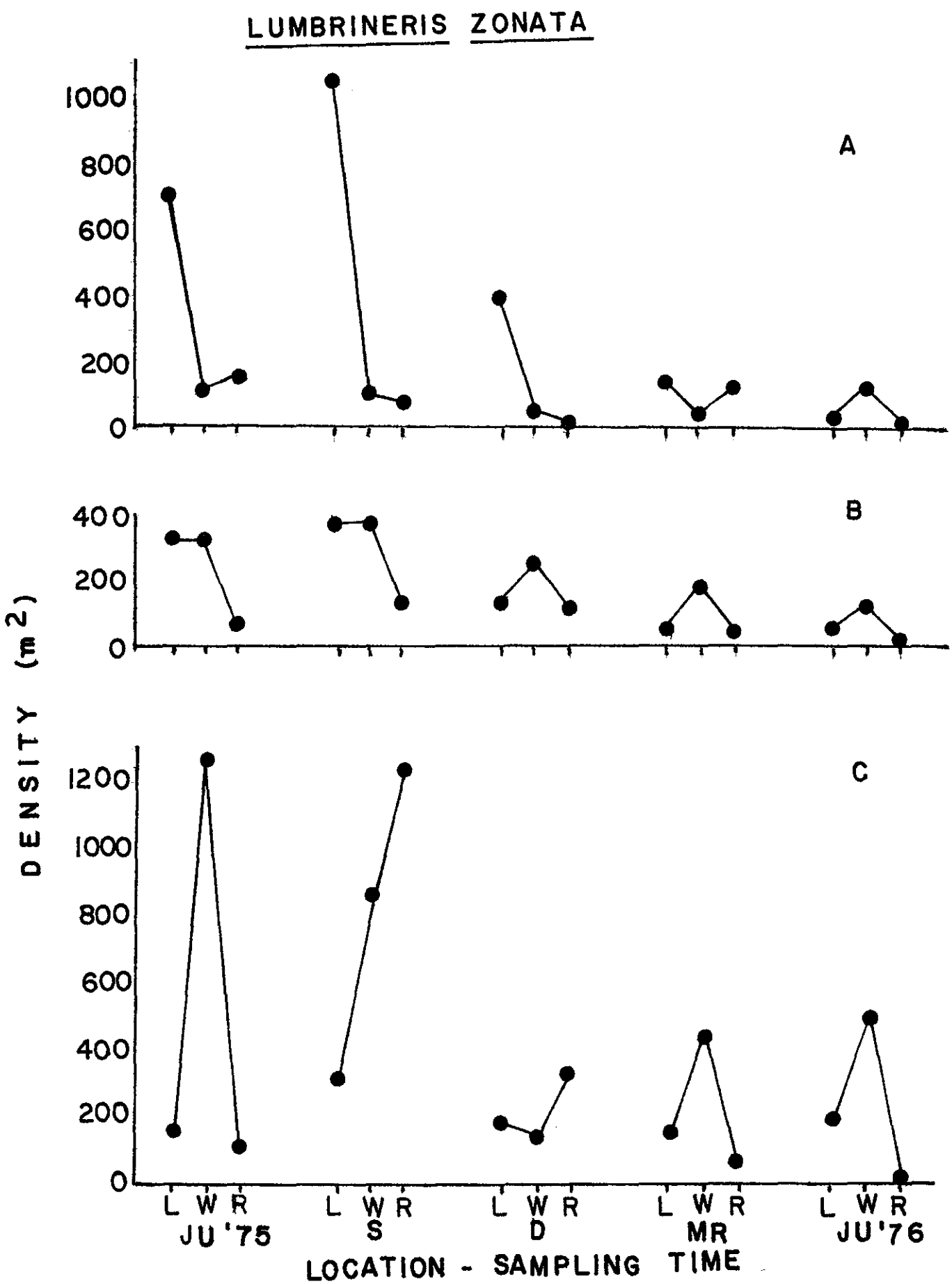

LUMBRINERIS ZONATA
1000
800
600
400
200
0
A
400
200
0
B
DENSITY (m2)
1200
1000
800
600
400
200
0
C
L W R
JU '75
L W R
S
L W R
D
L W R
MR
L W R
JU '76
LOCATION - SAMPLING TIME

FIGURE 23

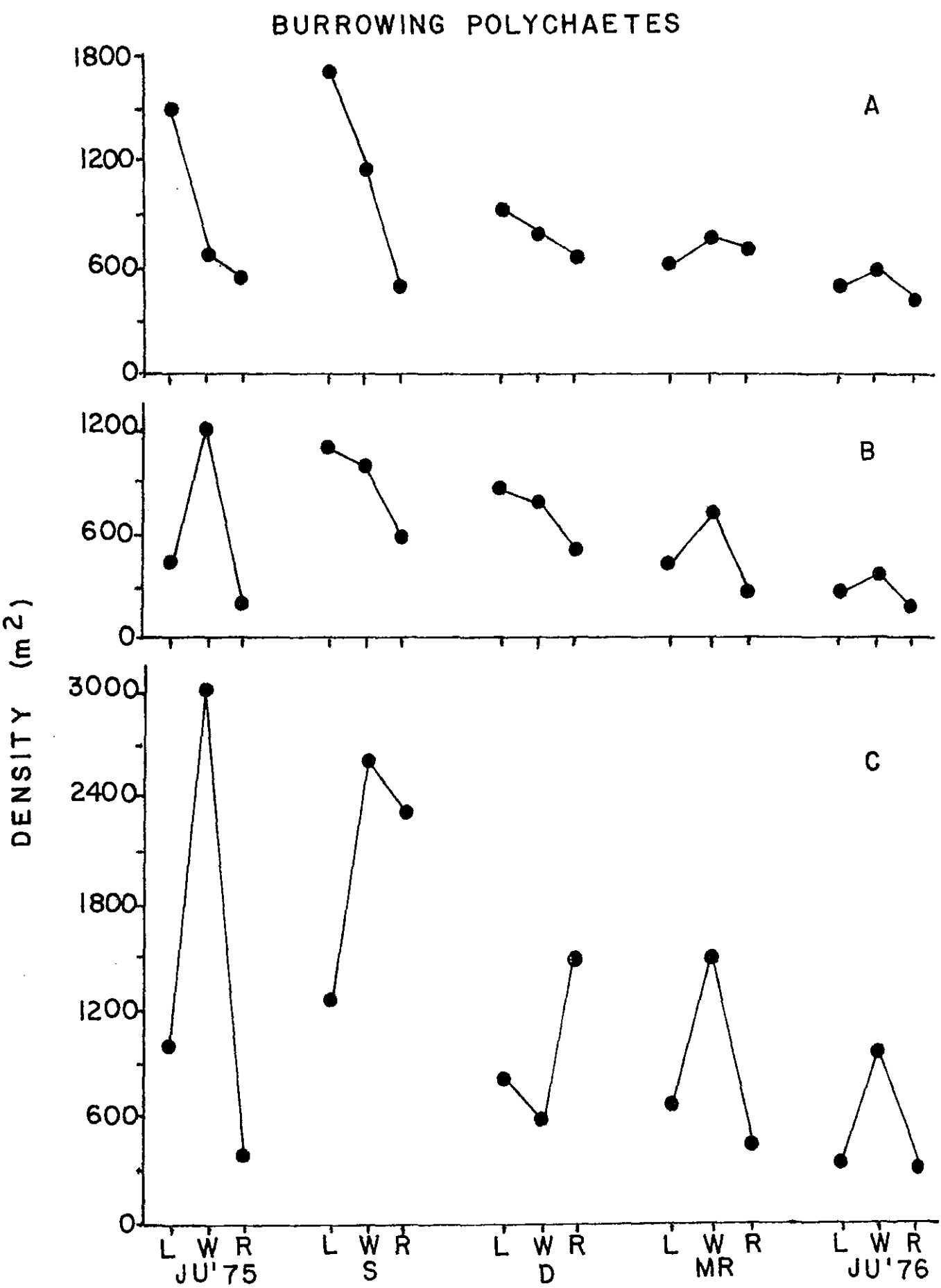

BURROWING POLYCHAETES
1800
1200
600
0
A
1200
600
0
B
3000
2400
1800
1200
600
0
C
DENSITY (m2)
L W R
JU'75
L W R
S
L W R
D
L W R
MR
L W R
JU'76
LOCATION - SAMPLING TIME

FIGURE 24

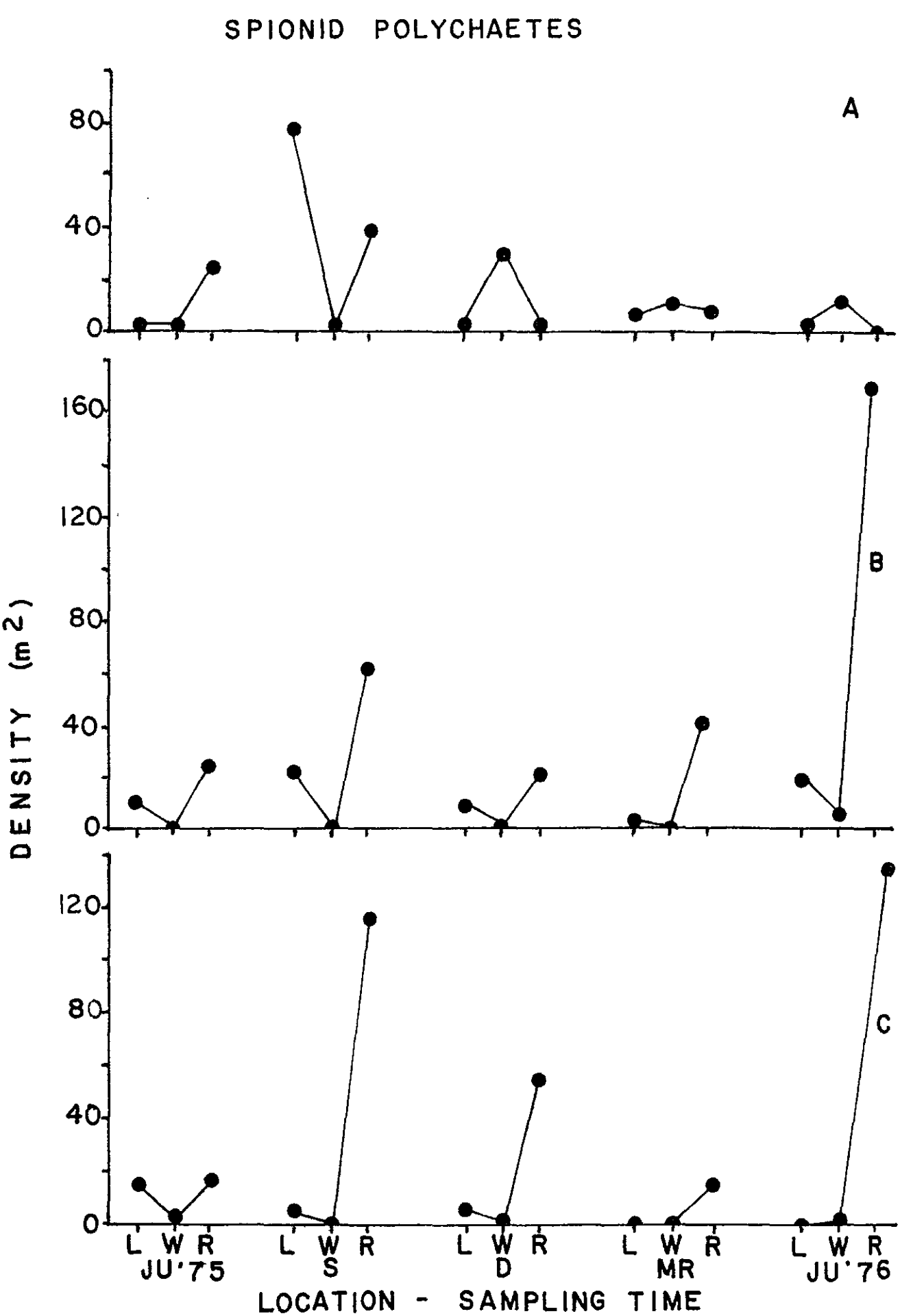

SPIONID POLYCHAETES
A
B
C
80
40
0
160
120
80
40
0
120
80
40
0
DENSITY (m2)
L W R
JU'75
L W R
S
L W R
D
L W R
MR
L W R
JU'76
LOCATION - SAMPLING TIME

FIGURE 25

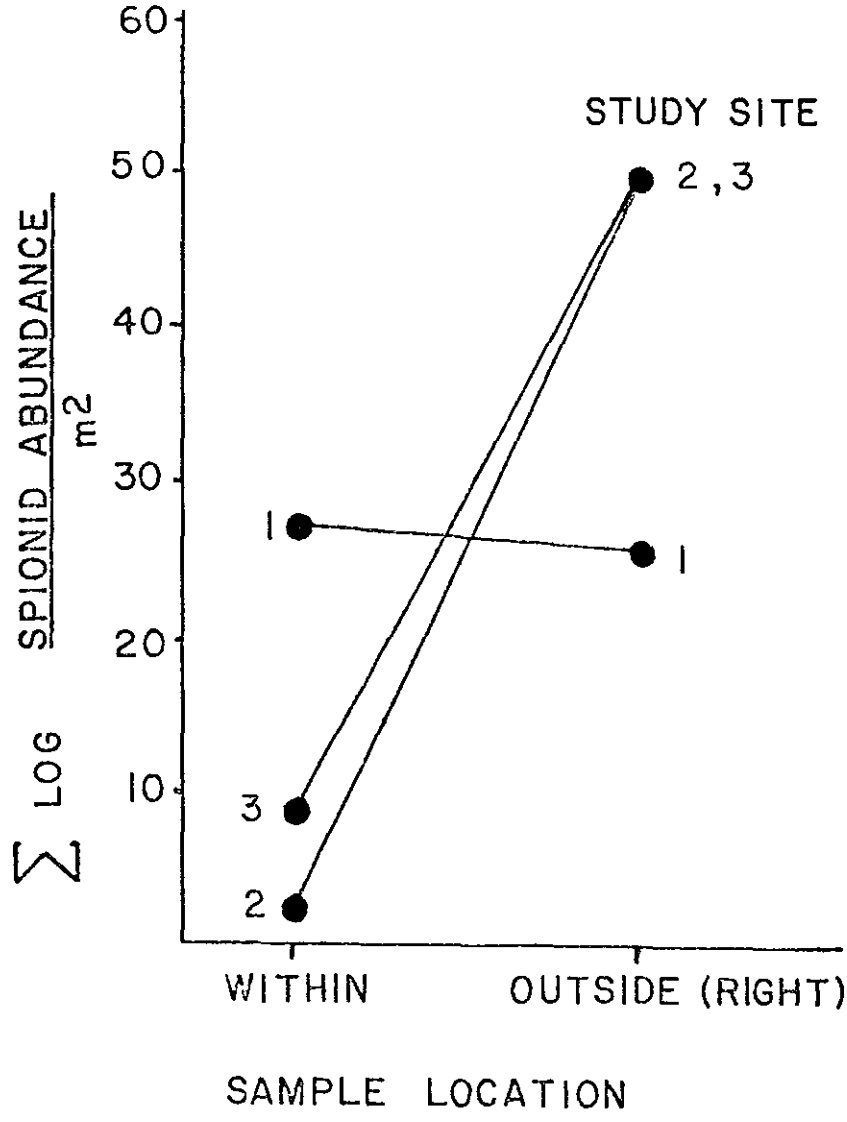

60
50
40
30
20
10
STUDY SITE
2,3
1
1
3
2
Σ LOG SPIONID ABUNDANCE / m2
WITHIN
OUTSIDE (RIGHT)
SAMPLE LOCATION

FIGURE 26

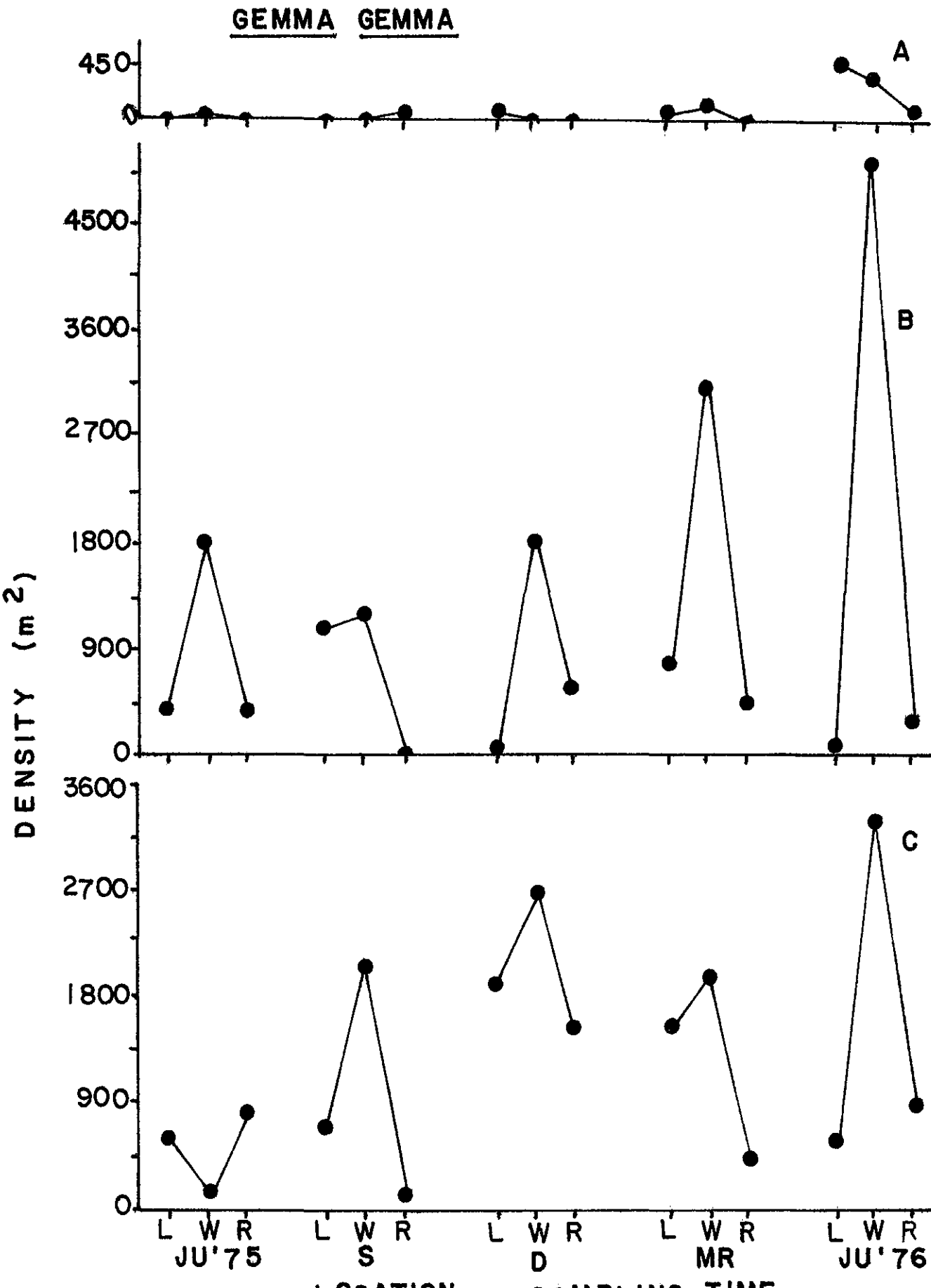

GEMMA GEMMA
A
450
0
B
4500
3600
2700
1800
900
0
C
3600
2700
1800
900
0
DENSITY (m 2)
L W R
JU'75
S
D
MR
JU'76
LOCATION - SAMPLING TIME

FIGURE 27

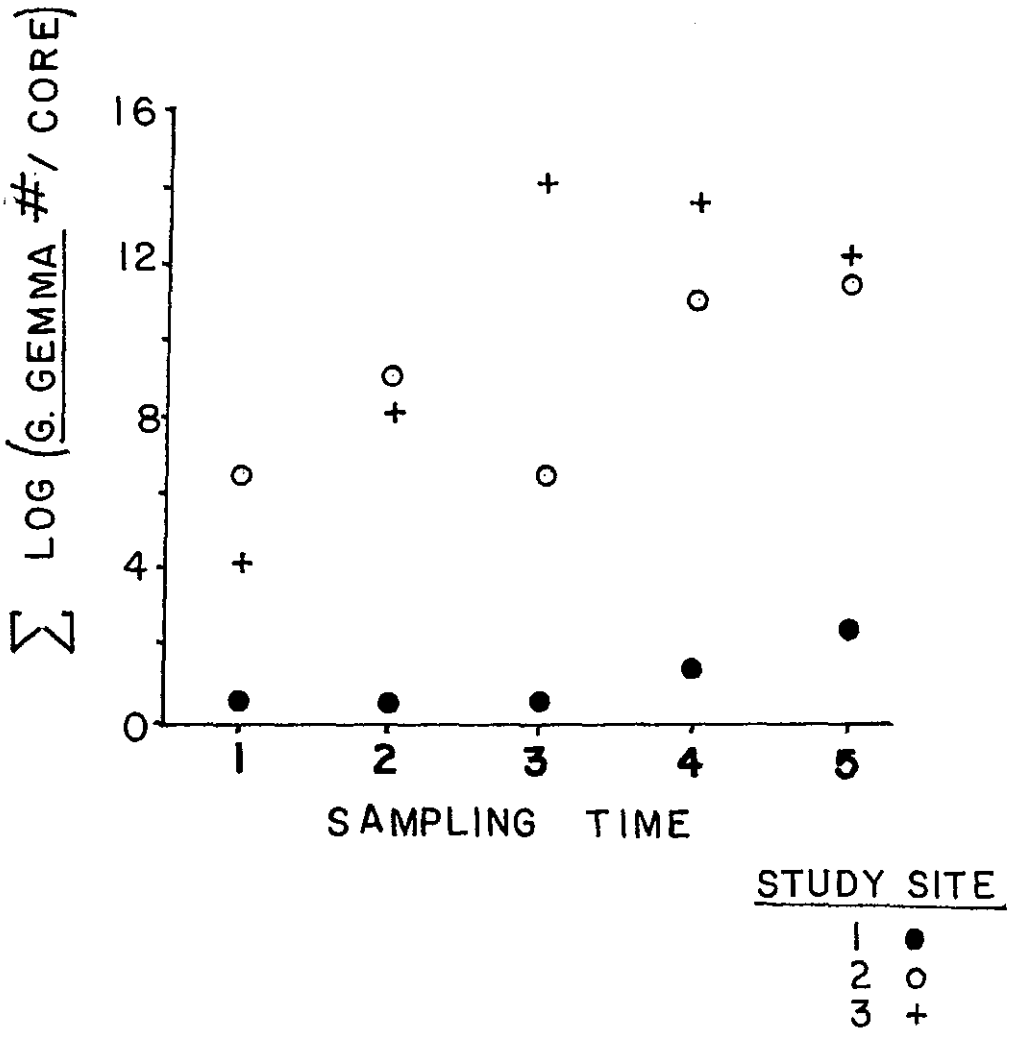

Σ LOG (G. GEMMA #/ CORE)
16
12
8
4
0
1
2
3
4
5
SAMPLING TIME
STUDY SITE
1
2
3

FIGURE 28

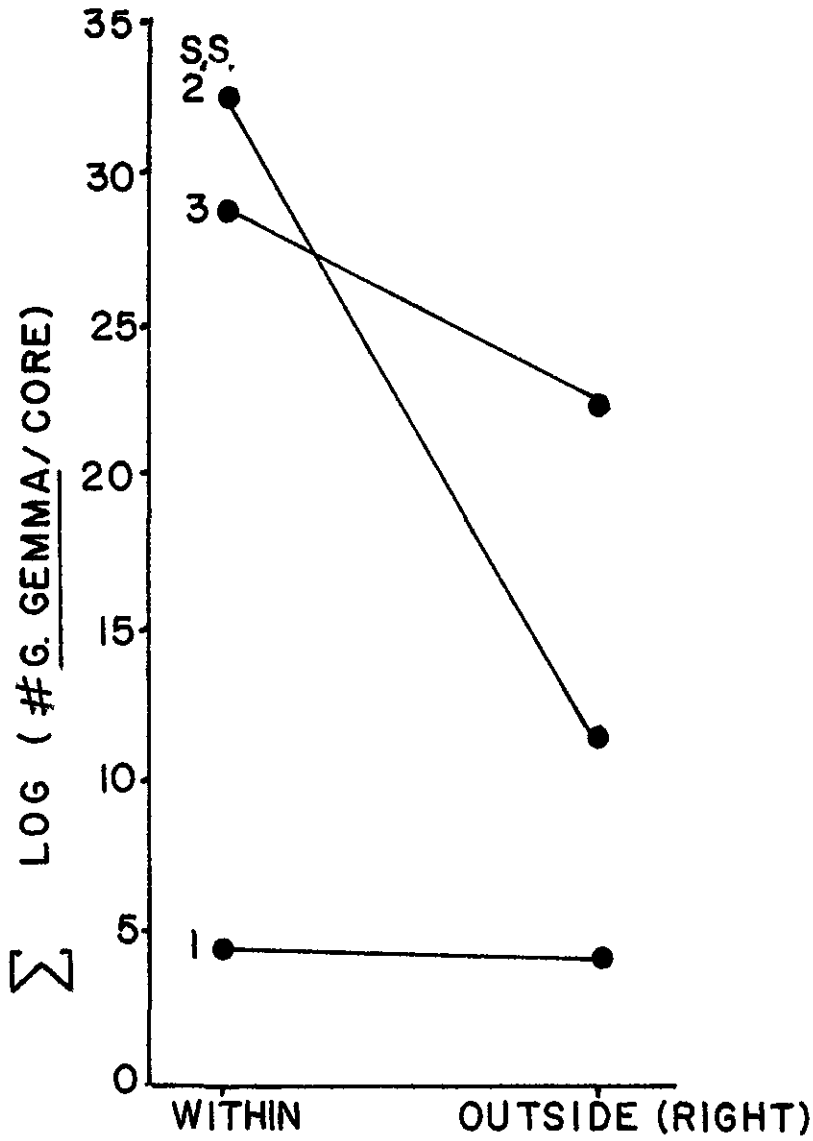

35
30
25
20
15
10
5
0
S.S.
2
3
1
Σ LOG (#G. GEMMA/ CORE)
WITHIN
OUTSIDE (RIGHT)
SAMPLE LOCATION

FIGURE 29

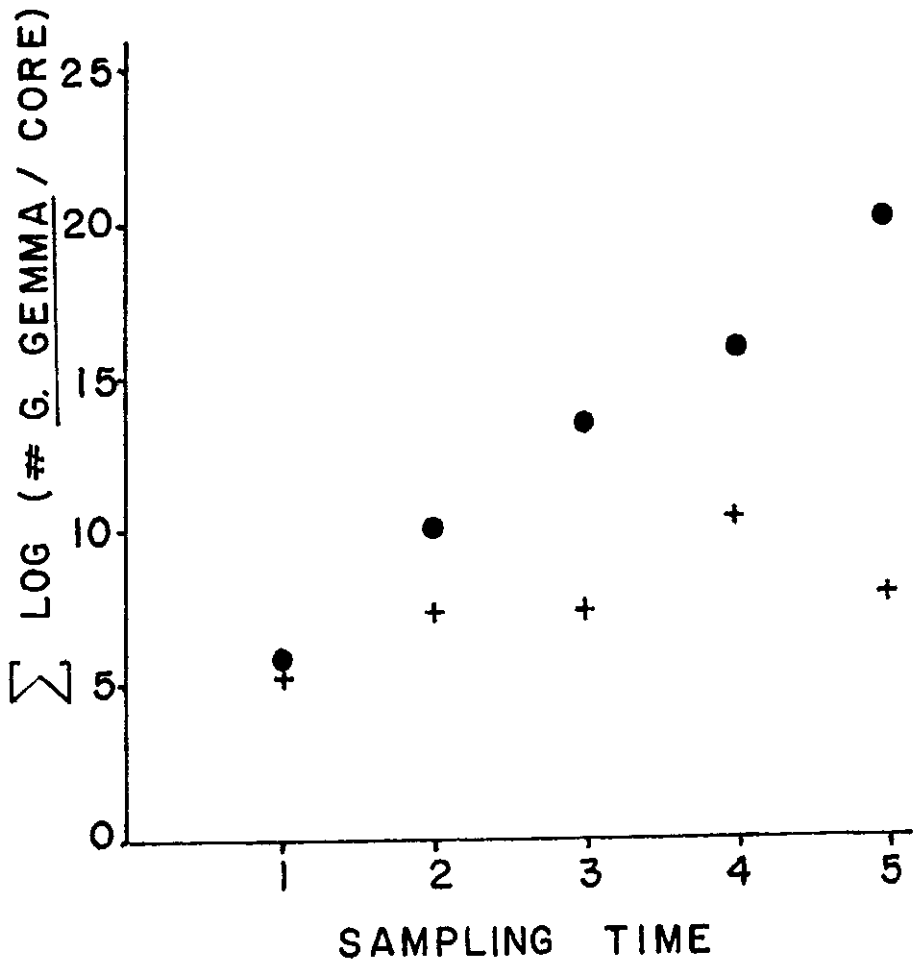

Σ LOG (# G. GEMMA / CORE)
25
20
15
10
5
0
1
2
3
4
5
SAMPLING TIME
LOCATION
WITHIN ●
OUTSIDE +

FIGURE 30

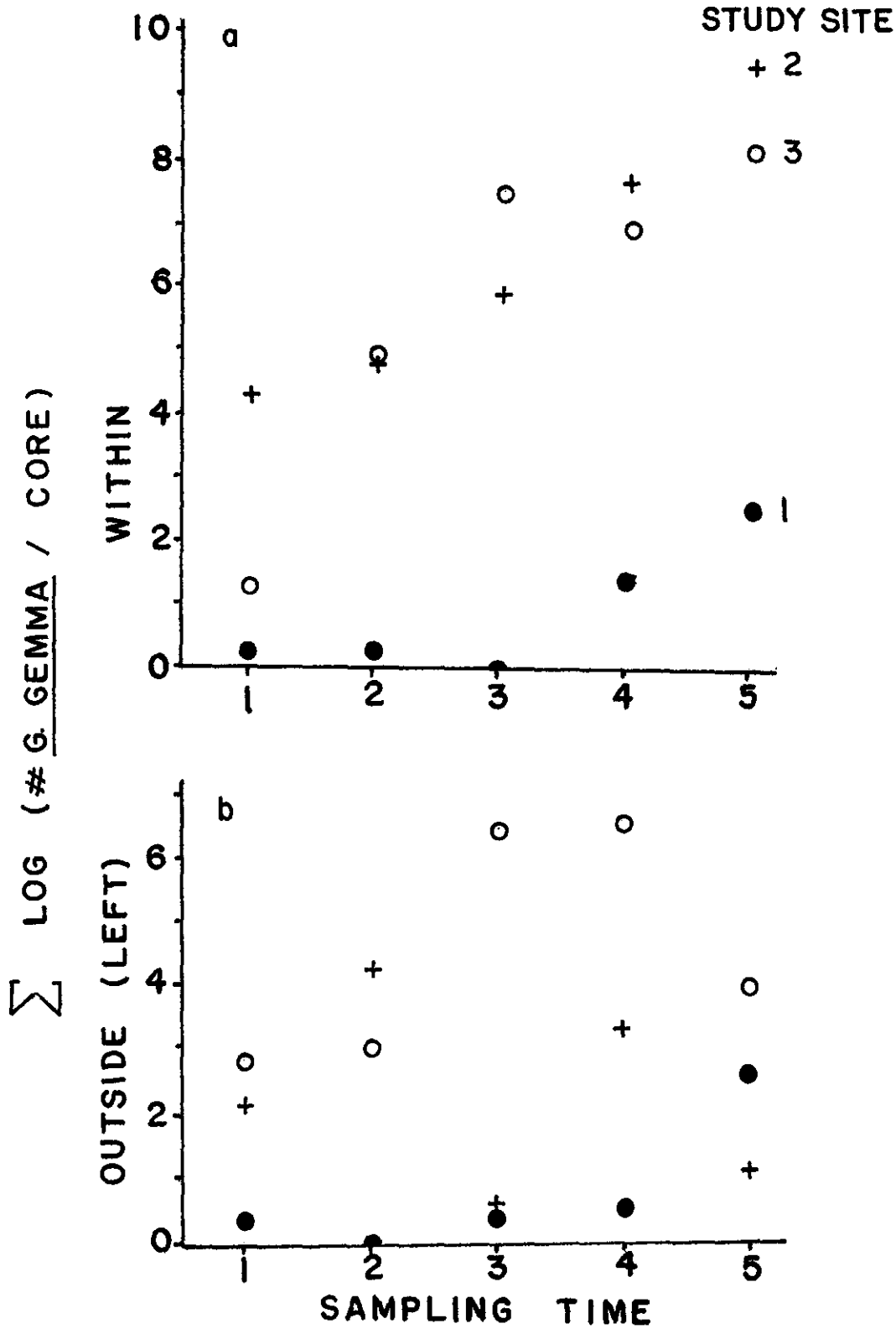

STUDY SITE
+ 2
o 3
● 1
a
b
WITHIN
OUTSIDE (LEFT)
Σ LOG (# G. GEMMA / CORE)
SAMPLING TIME
0
2
4
6
8
10
1
2
3
4
5

FIGURE 31

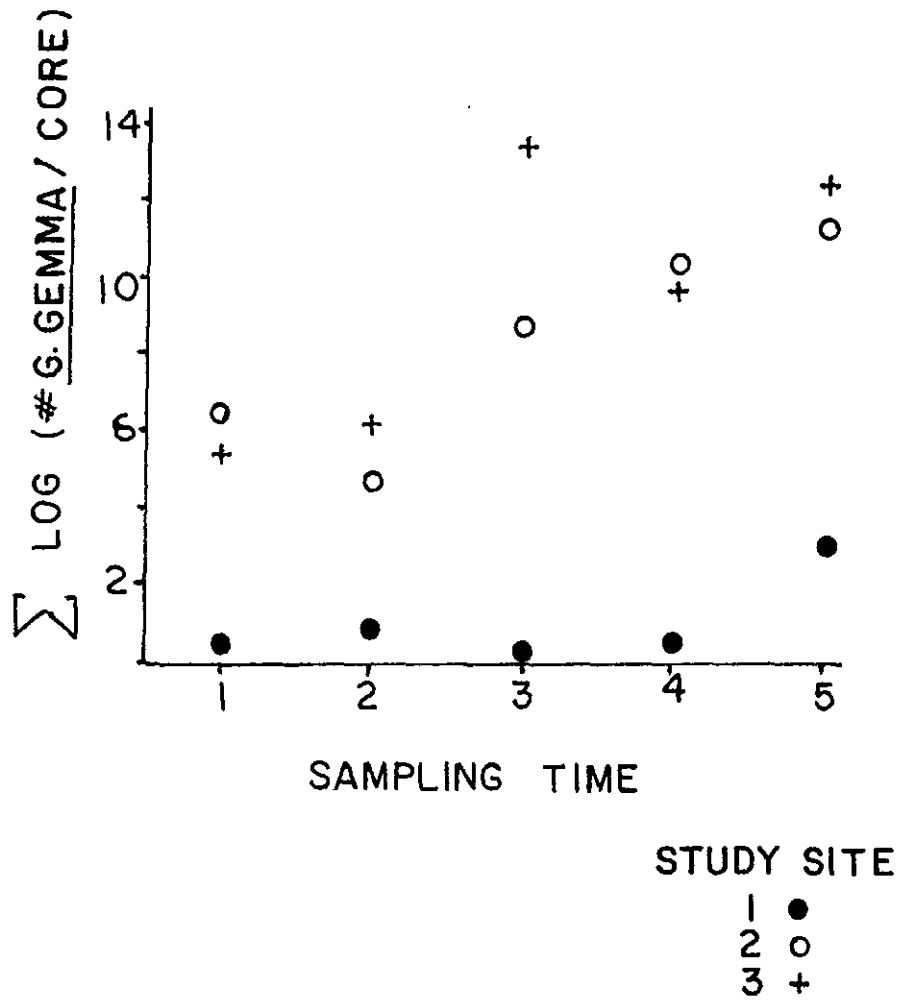

Σ LOG (# G. GEMMA / CORE)
14
10
6
2
1
2
3
4
5
SAMPLING TIME
STUDY SITE
1 ●
2 o
3 +

FIGURE 32

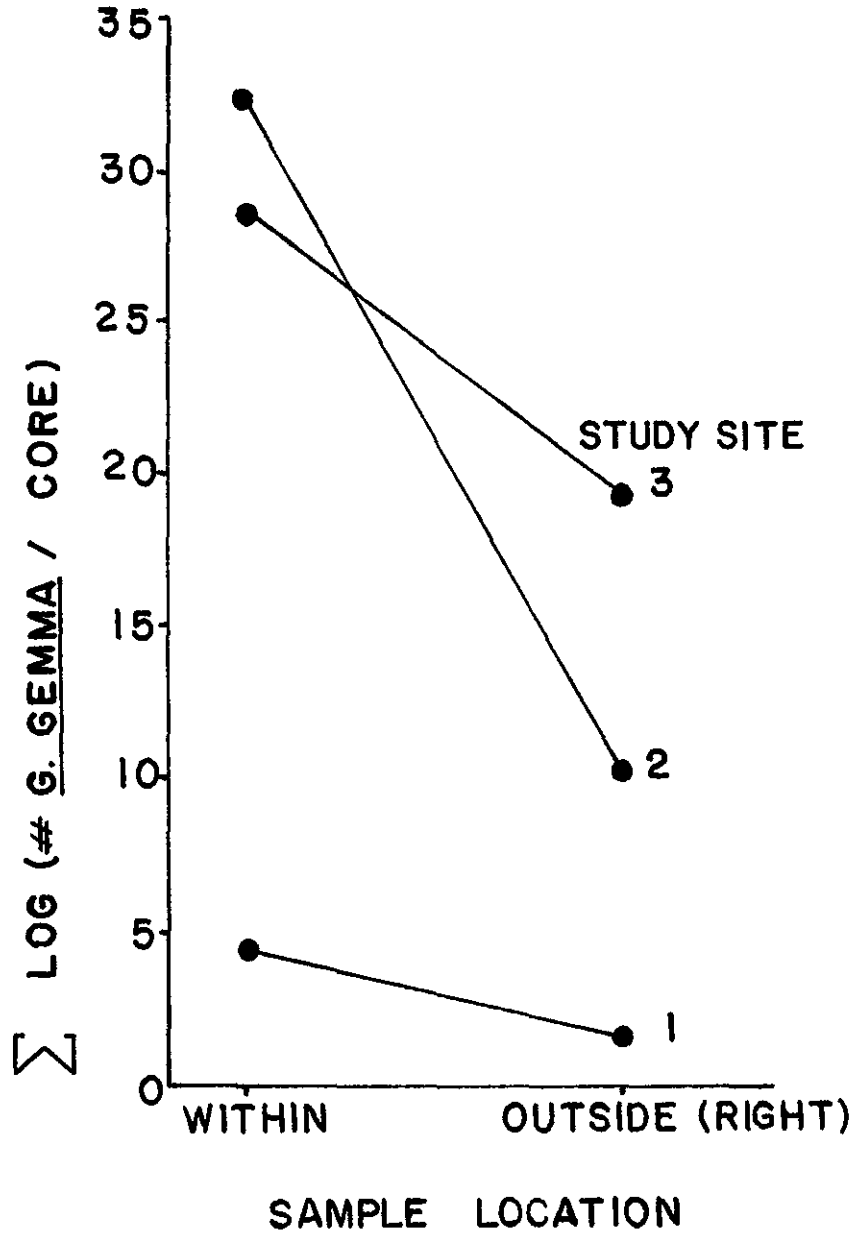

35
30
25
20
15
10
5
0
Σ LOG (# G. GEMMA / CORE)
STUDY SITE
3
2
1
WITHIN
OUTSIDE (RIGHT)
SAMPLE LOCATION

FIGURE 33

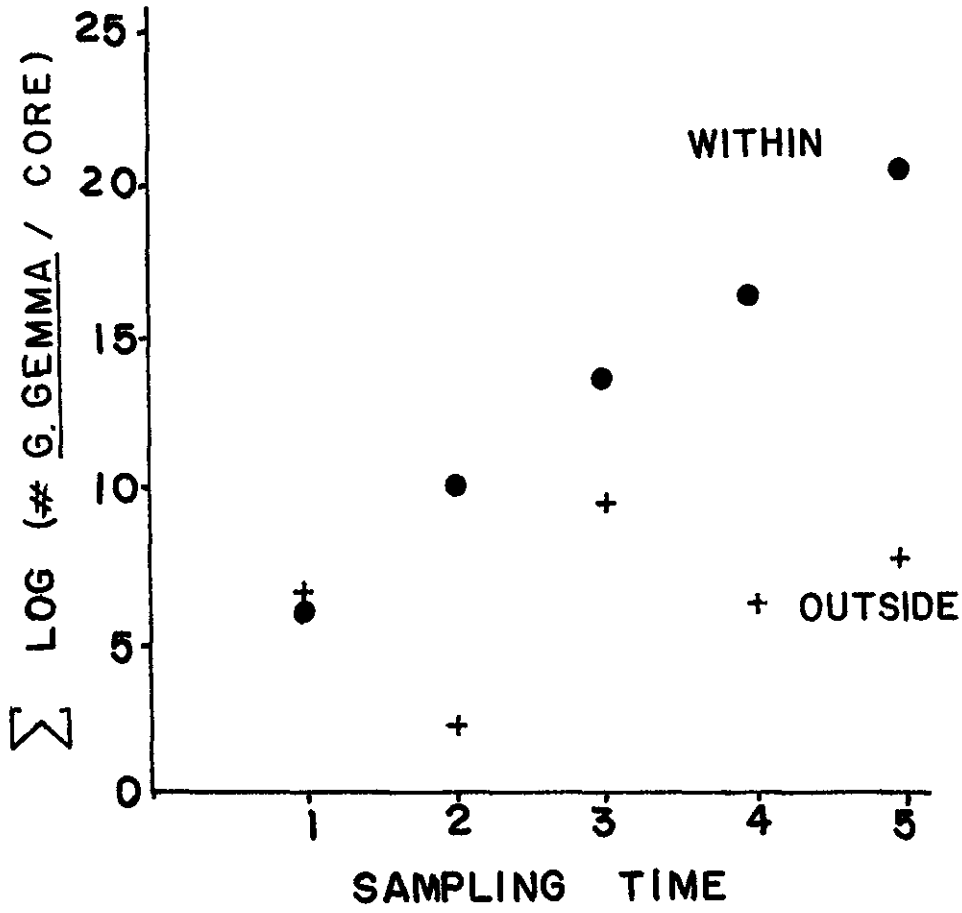

25
20
15
10
5
0
LOG (# G. GEMMA / CORE)
WITHIN
OUTSIDE
1
2
3
4
5
SAMPLING TIME

FIGURE 34

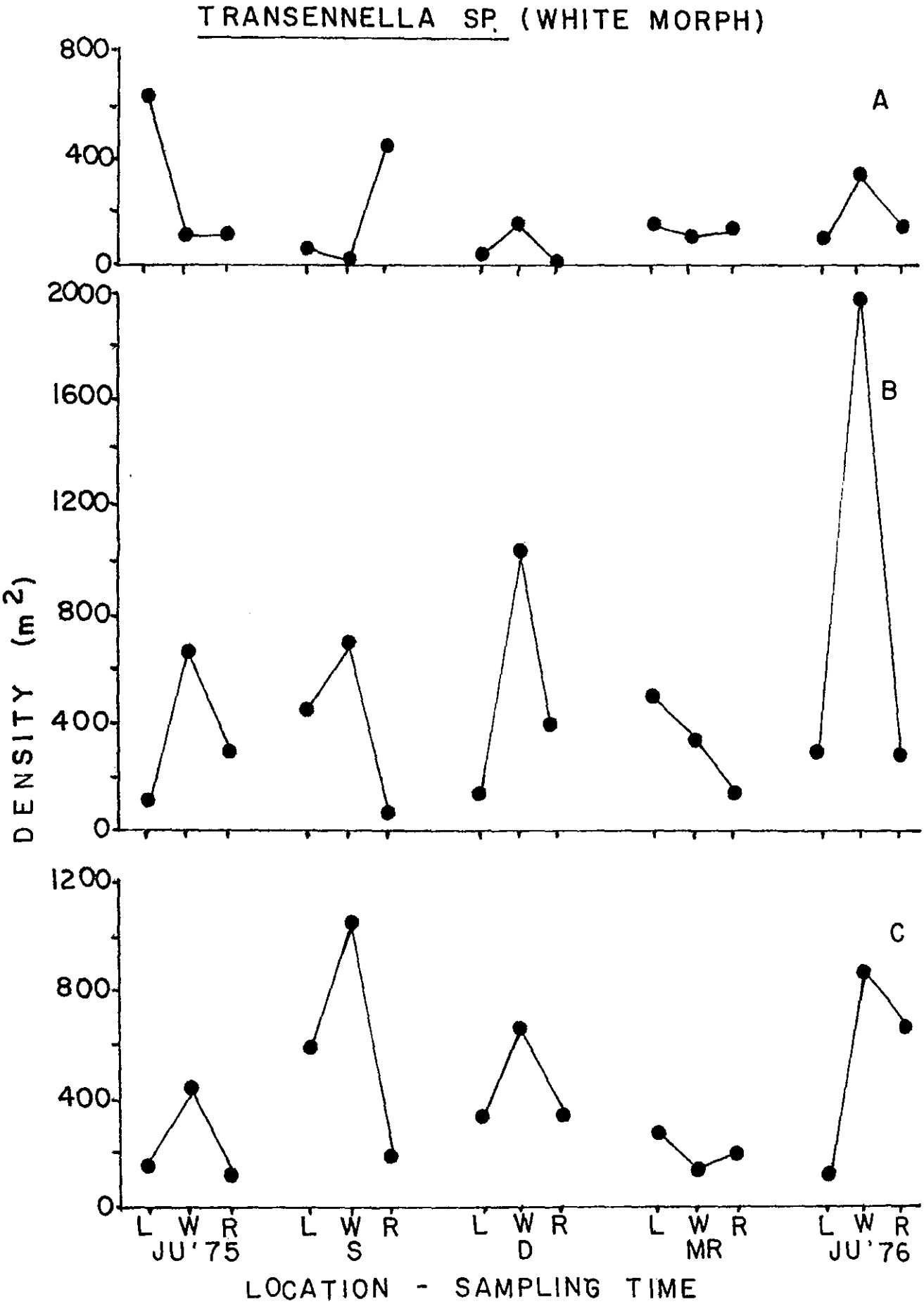

TRANSENNELLA SP. (WHITE MORPH)
800
400
0
A
2000
1600
1200
800
400
0
B
DENSITY (m2)
1200
800
400
0
C
L W R
JU '75
L W R
S
L W R
D
L W R
MR
L W R
JU '76
LOCATION - SAMPLING TIME

FIGURE 35

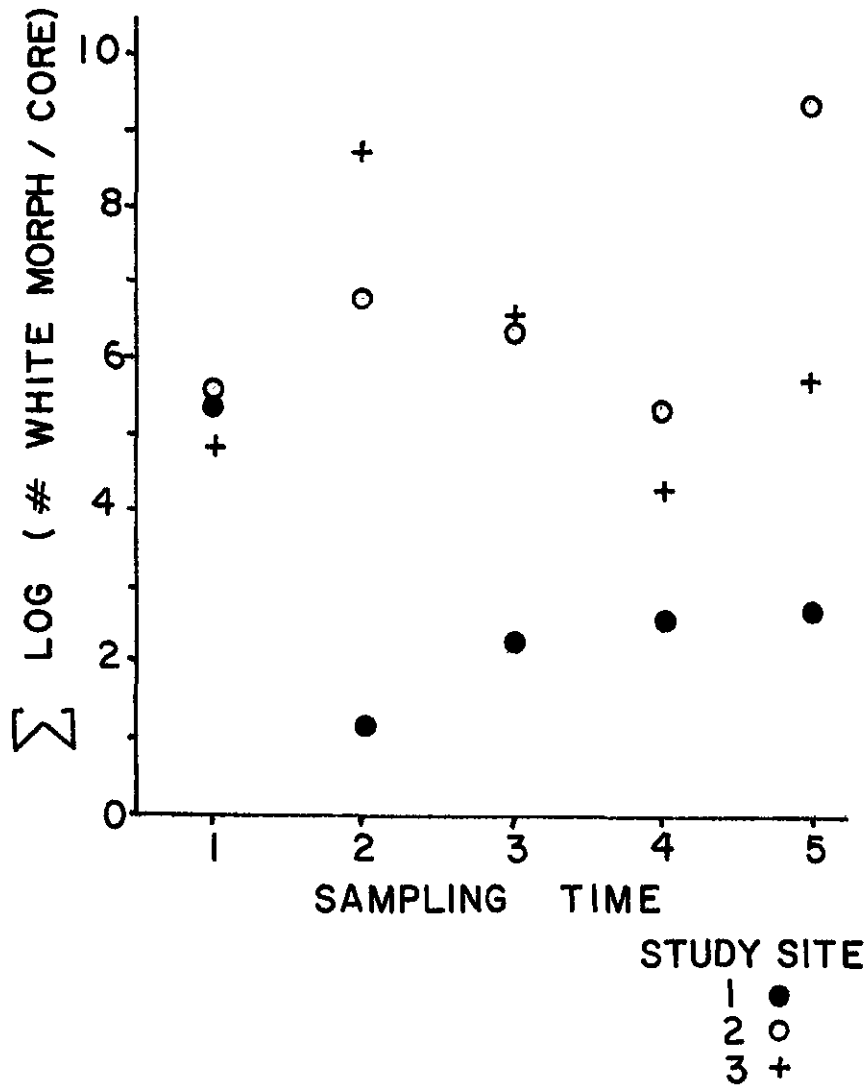

Σ LOG (# WHITE MORPH / CORE)
0
2
4
6
8
10
1
2
3
4
5
SAMPLING TIME
STUDY SITE
1
2
3

FIGURE 36

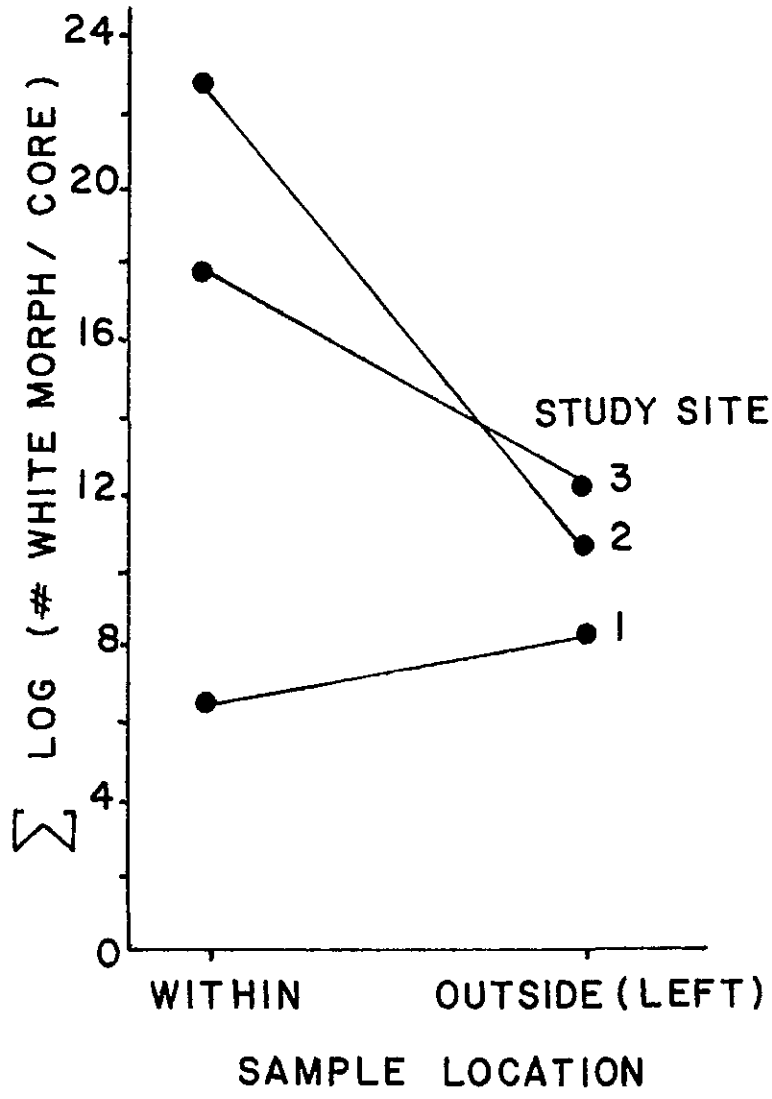

24
20
16
12
8
4
0
LOG (# WHITE MORPH / CORE)
STUDY SITE
3
2
1
WITHIN
OUTSIDE (LEFT)
SAMPLE LOCATION

FIGURE 37

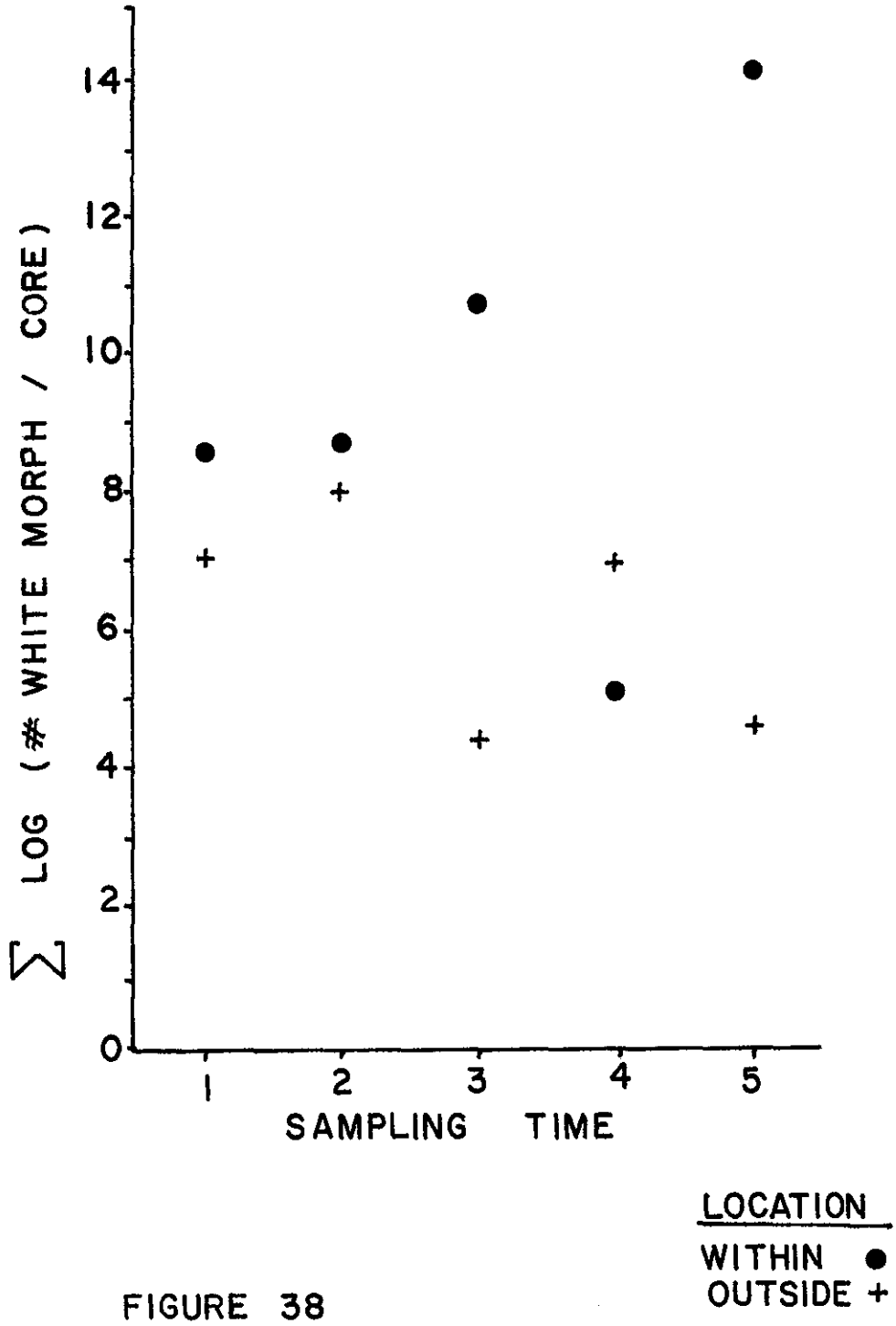

Σ LOG (# WHITE MORPH / CORE)
0
2
4
6
8
10
12
14
1
2
3
4
5
SAMPLING TIME
LOCATION
WITHIN ●
OUTSIDE +

FIGURE 38

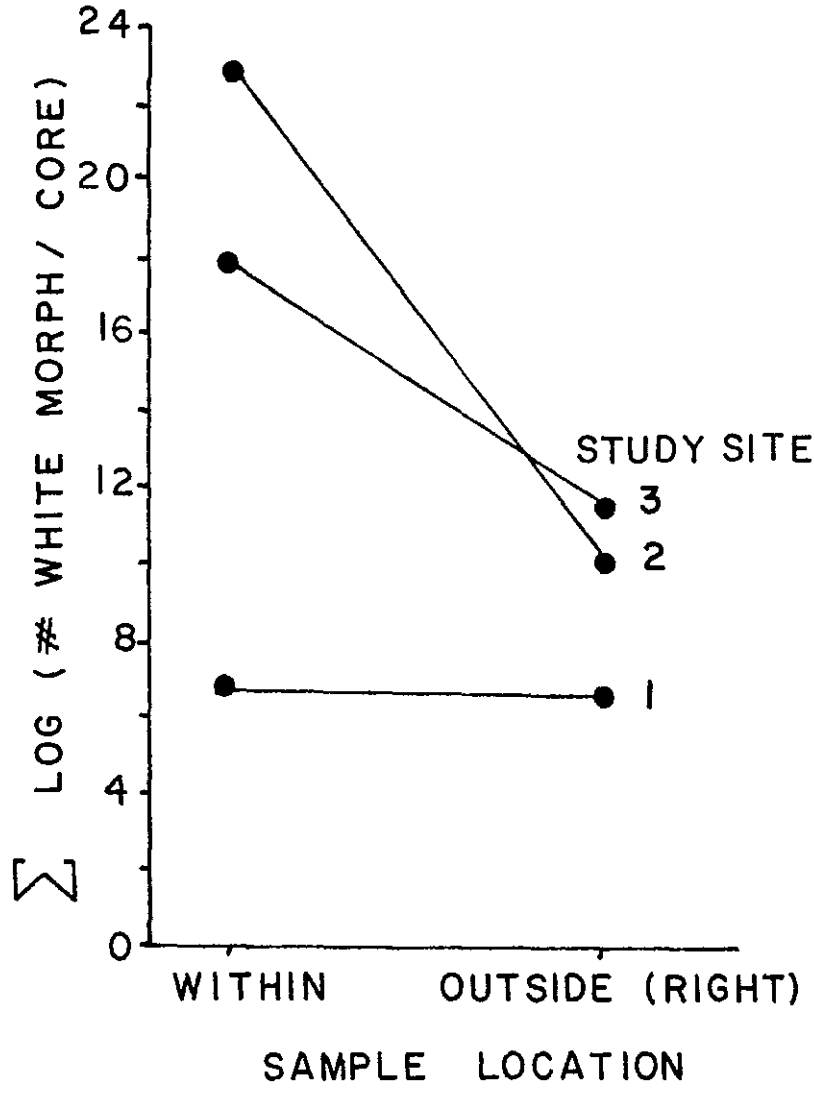

24
20
16
12
8
4
0
Σ LOG (# WHITE MORPH / CORE)
STUDY SITE
3
2
1
WITHIN
OUTSIDE (RIGHT)
SAMPLE LOCATION

FIGURE 39

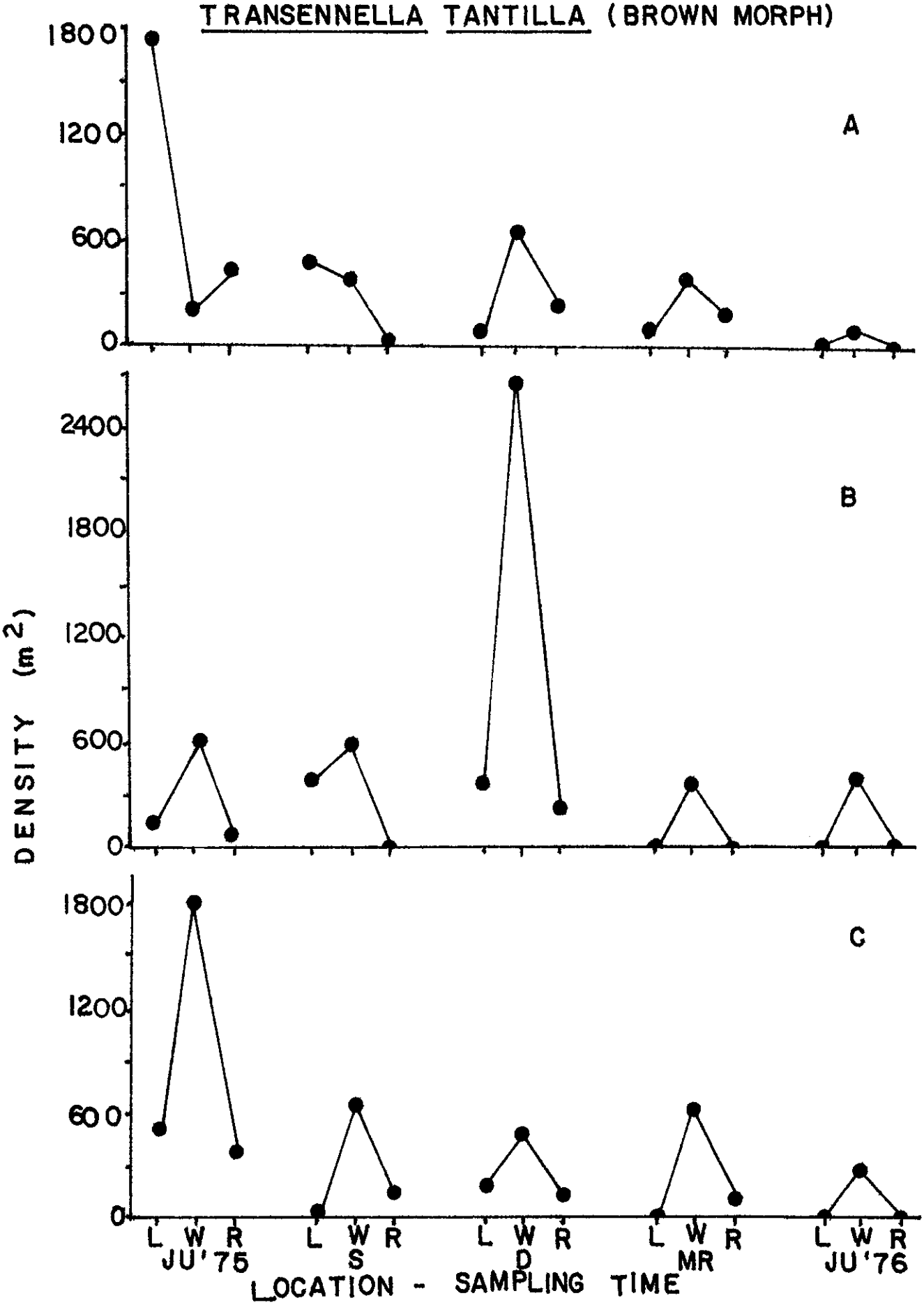

TRANSENNELLA TANTILLA (BROWN MORPH)
1800
1200
600
0
A
2400
1800
1200
600
0
B
DENSITY (m²)
1800
1200
600
0
C
L W R
JU '75
L W R
S
L W R
D
L W R
MR
L W R
JU '76
LOCATION - SAMPLING TIME

FIGURE 40

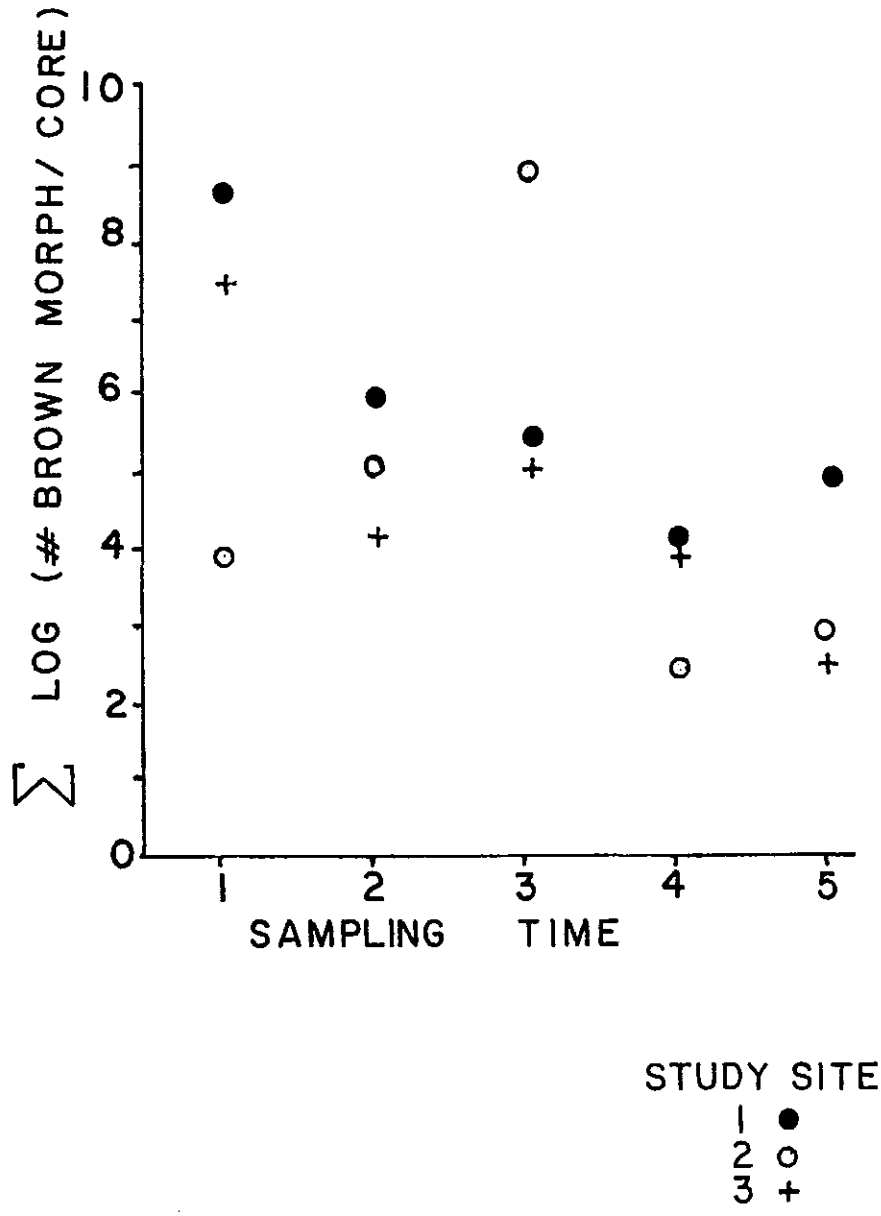

Σ LOG (# BROWN MORPH/ CORE)
10
8
6
4
2
0
1
2
3
4
5
SAMPLING TIME
STUDY SITE
1 ●
2 o
3 +

FIGURE 41

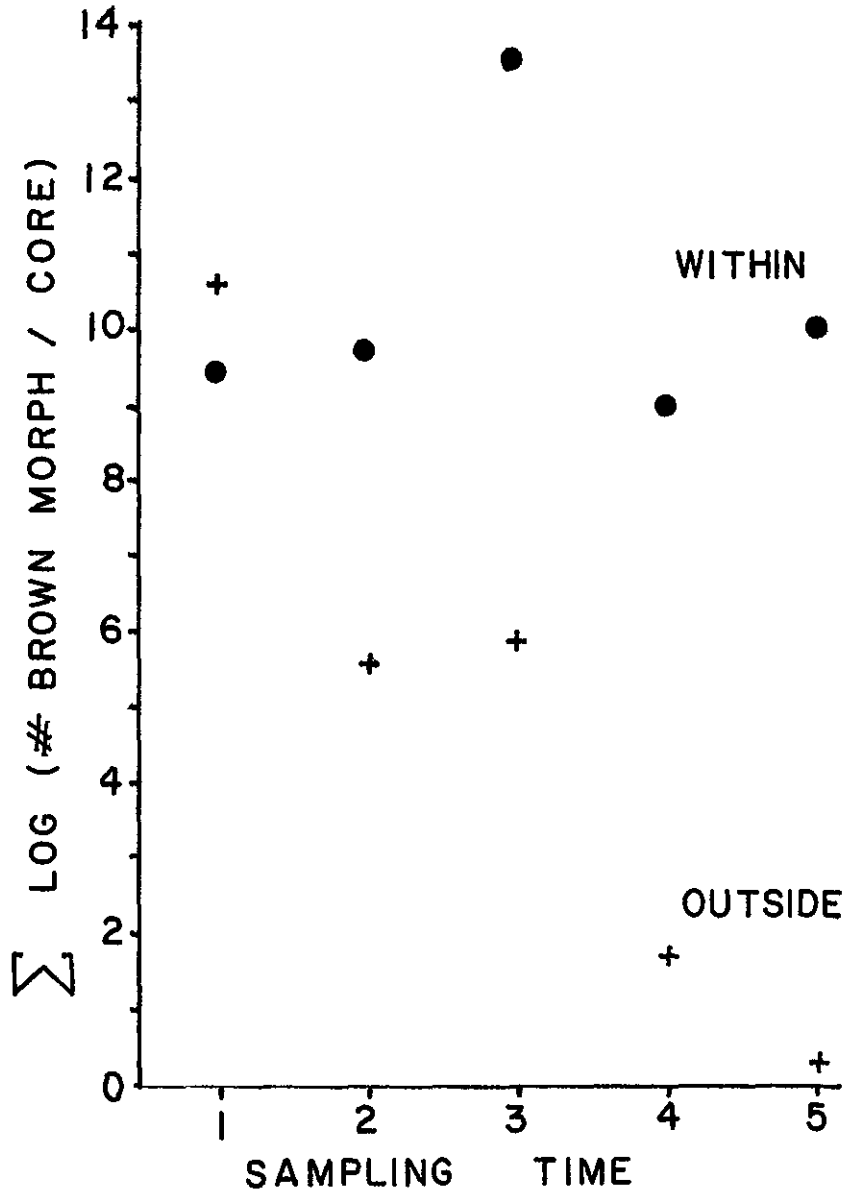

14
12
10
8
6
4
2
0
Σ LOG (# BROWN MORPH / CORE)
WITHIN
OUTSIDE
1
2
3
4
5
SAMPLING TIME

FIGURE 42

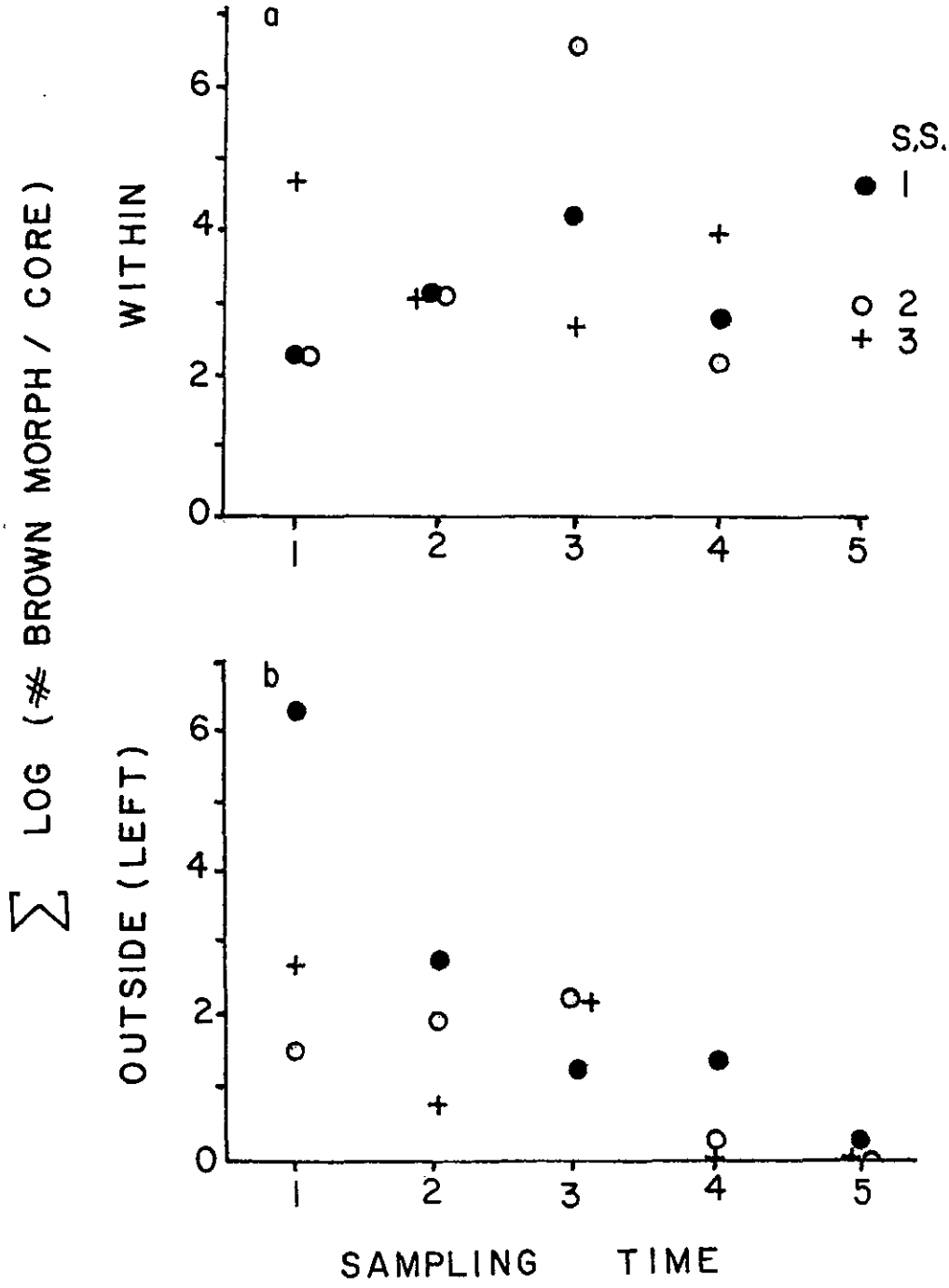

a
b
WITHIN
OUTSIDE (LEFT)
Σ LOG (# BROWN MORPH / CORE)
S.S.
1
2
3
0
2
4
6
1
2
3
4
5
SAMPLING TIME

FIGURE 43

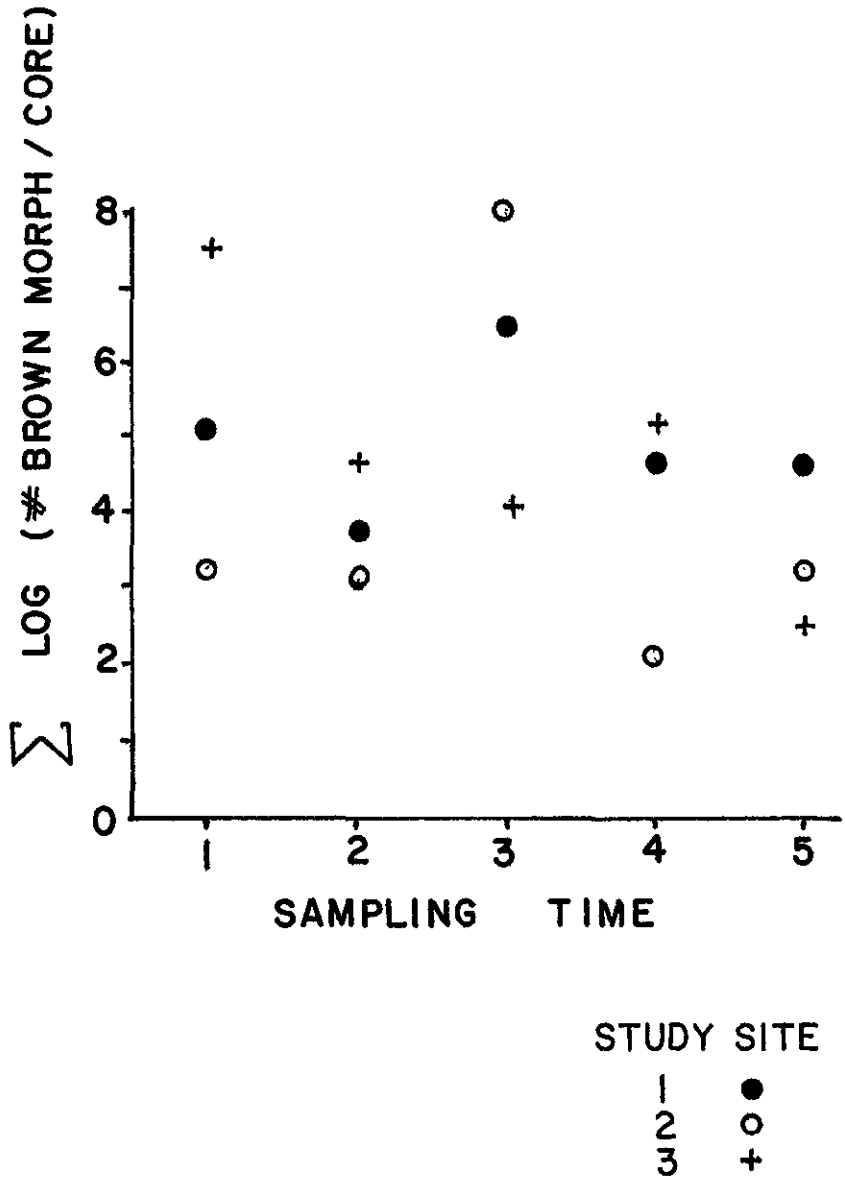

∑ LOG (# BROWN MORPH / CORE)
0
2
4
6
8
1
2
3
4
5
SAMPLING TIME
STUDY SITE
1
2
3

FIGURE 44

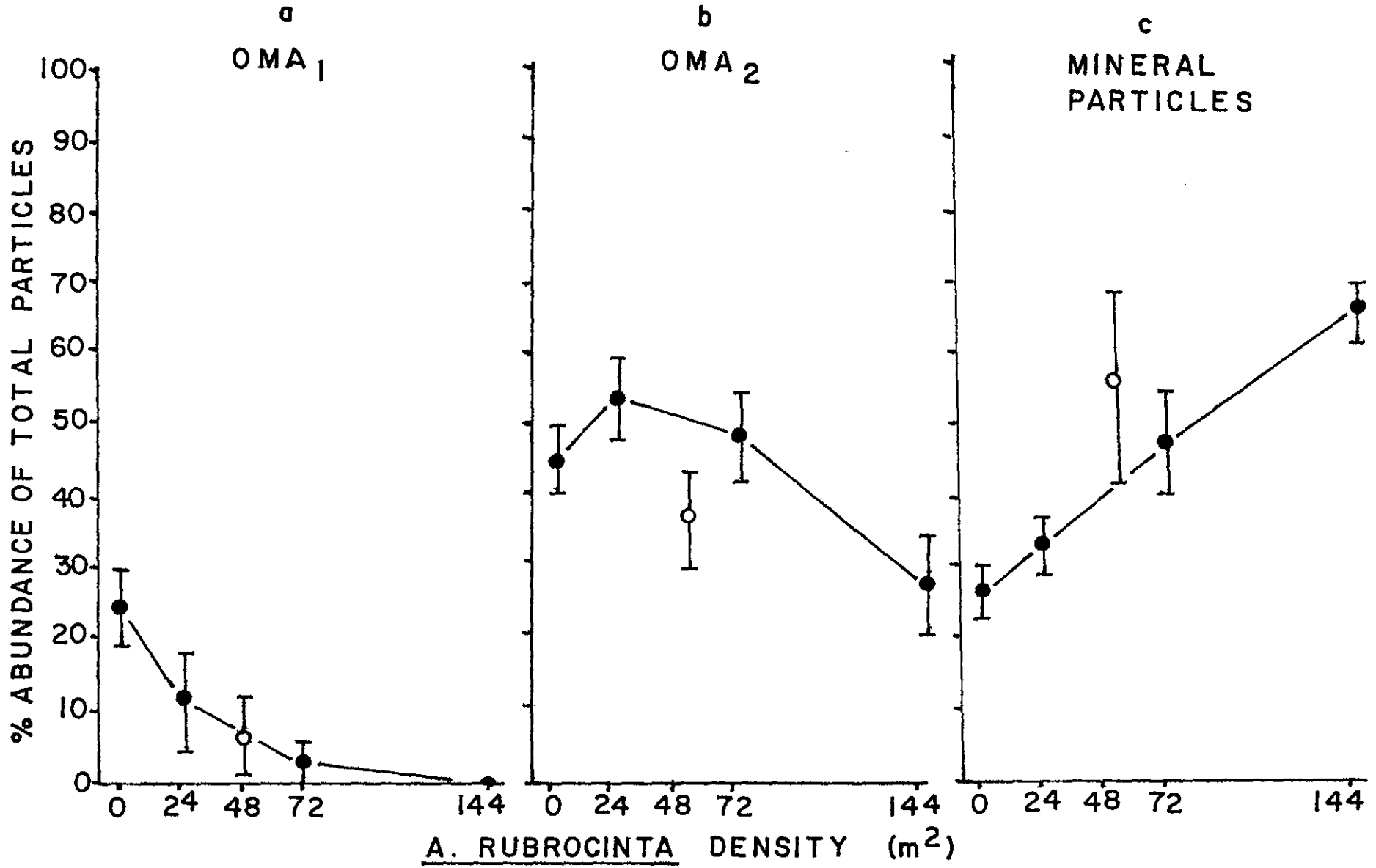
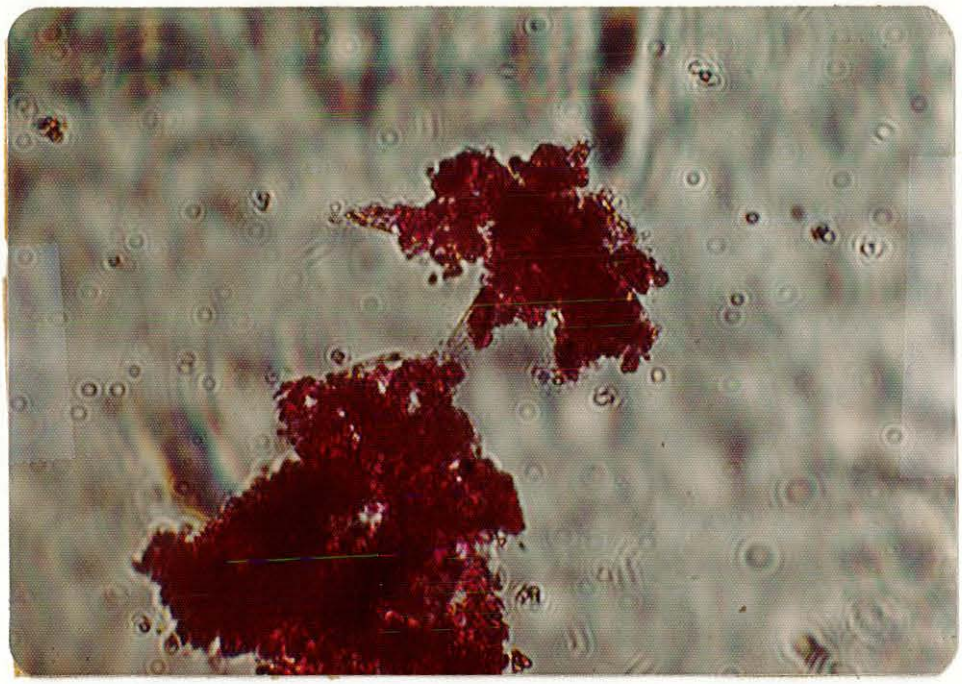
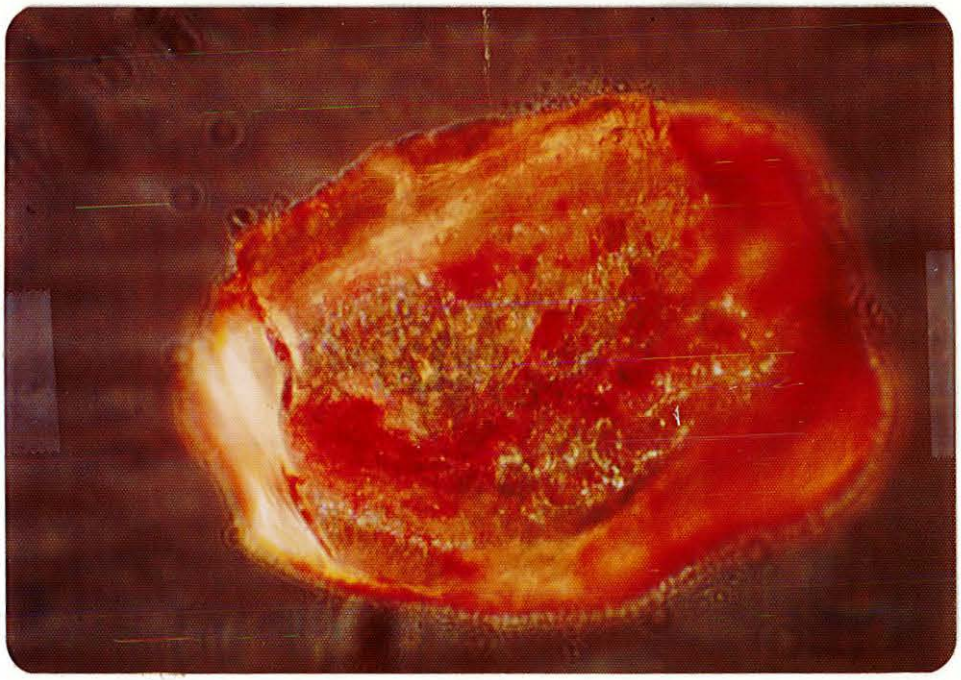

a
OMA 1
b
OMA 2
c
MINERAL PARTICLES
% ABUNDANCE OF TOTAL PARTICLES
100
90
80
70
60
50
40
30
20
10
0
0 24 48 72 144
0 24 48 72 144
0 24 48 72 144
A. RUBROCINTA DENSITY (m2)

FIGURE 45

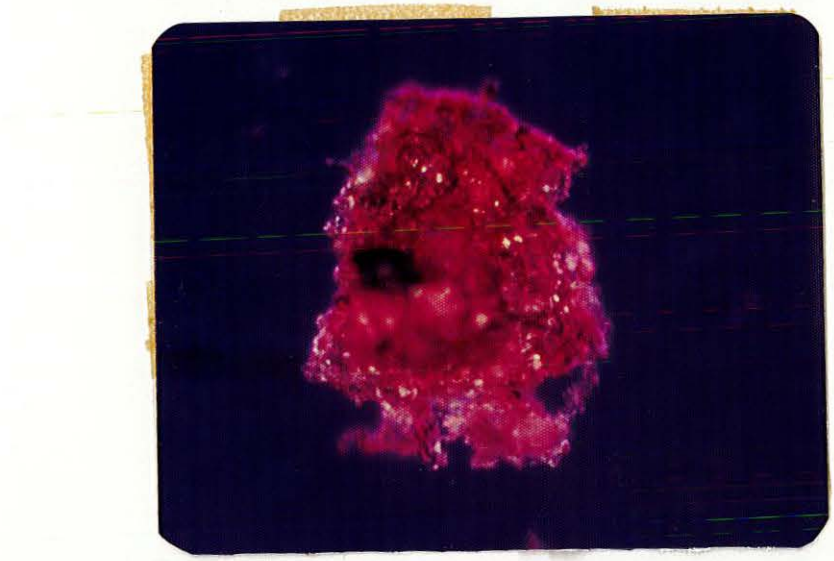


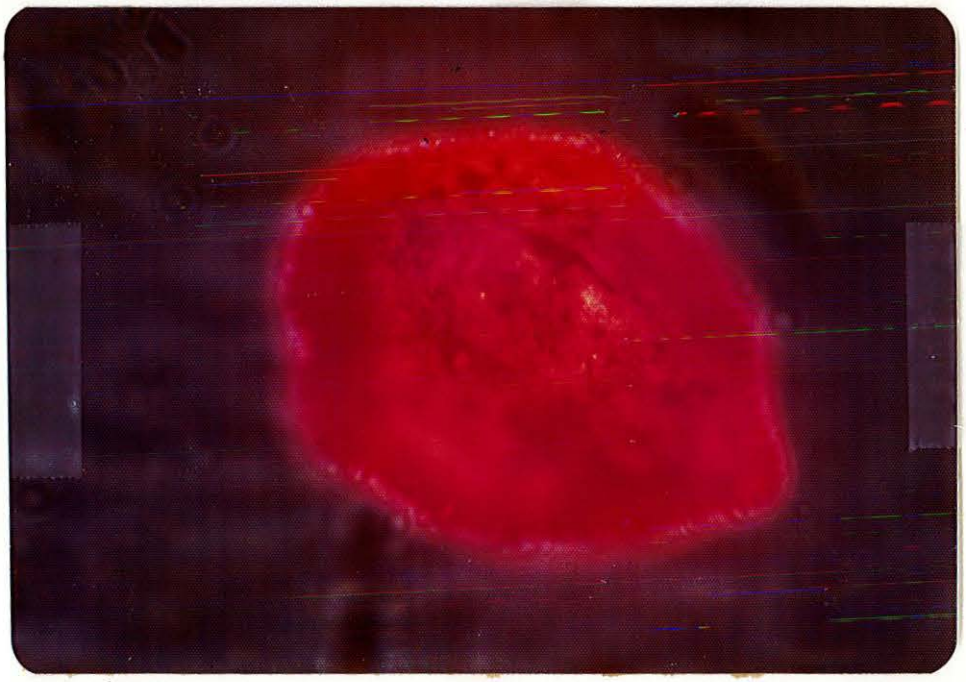
a. OMA_1 (LOOSE FLOC) - 300x



c. QUARTZ MINERAL PARTICLE - 300x

FIG. 46





b. OMA_2 (COMPACT FLOC, 2 TYPES) - 300x

FIG. 46